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Modelling the Distribution and Breeding Performance of the Raven *Corvus Corax* in Relation to Habitat:

An application using satellite remote sensing and Geographical Information Systems

By

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This thesis is submitted in candidature for the Degree of Doctor of Philosophy,

Department of Zoology, The University of Glasgow.

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" In short, ravens are near the bottom of the list

as a sane choice for a research project.'

Professor Bernd Heinrich, 1990

Ravens in Winter

ACKNOWLEDGEMENTS

I owe a great deal to many people, especially as large parts of the work were collaborative. First I would like to thank my supervisor Dr. David Houston for his advice, encouragement and help throughout the project. The study was funded by the Nature Conservancy Council, Scotland (now Scottish Natural Heritage) and I am grateful to Dr. Des Thompson for his supervision from that end, and for agreeing to fund the additional work in Wales. Thanks to Professors Steven Phillips and Graham Coombs for the use of departmental facilities in Glasgow. Thanks also to Professor David Crompton for facilities in the computing laboratory where much of this thesis was written.

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To my Mom and Dad, Eric and Annetta Thomas.

DECLARATION

I declare that the work described in this thesis has been carried out by myself unless otherwise cited or acknowledged. It is entirely of my own composition and has not, in whole or in part, been submitted for any other degree.

Christopher James Thomas

March 1993

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SUMMARY

1. In this thesis I develop statistical predictive models of spatial variation in raven (*Corvus corax*) occupation and breeding performance in relation to habitat, using satellite remotely sensed images and Geographical Information Systems (GIS)

2. The study took place in mid-Argyll, in the south-western Highlands of Scotland, with fieldwork conducted in 1989 to 1991. The distribution and performance of breeding ravens were studied in a large area (c.6000km^2) where 235 past or present breeding sites were identified. The average density of breeding pairs in 1990 was 3.6 pairs/100km^2. Additional data from a higher density population in mid-Wales (11.1 pairs/100km^2) were provided by A.C. Cross.

3. Regression techniques were used to estimate timing of laying from measurements of eggs and chicks. It was not possible to produce equations with sufficient precision from egg measurements. Estimates were made to within ±3 days using morphometric measurements from nestlings .

4. I investigated the general relationship between the species and its environment in Britain using a comparative approach. A comparison was made of density and breeding performance of ravens in mid-Wales and mid-Argyll using the detailed and compatible data acquired in this study, followed by an analysis of these data combined with published accounts from elsewhere. Both analyses were in agreement: ravens occur at a great range of densities throughout Britain, but breeding performance was not related to breeding density. There was no evidence that breeding performance was influenced by habitat when populations were considered.

5. When considering breeding performance of individual pairs, previous studies found that breeding performance was adversely affected by afforestation in some regions but not others. Using evidence from several studies I argue that this does not contradict the conclusion above because habitat change in some areas

may have occurred at a faster pace than a new stable distribution of pairs could arise, given the traditional nature of raven territories. Variations in the turnover of territorial birds, the availability of nest sites and number of potential recruits to the breeding population may account for differences between studies.

6. There was evidence that there was a shortage of recruits in mid-Argyll and other areas, and that gaps in the raven distribution in mid-Argyll may have been due to a shortage of ravens rather than unsuitable habitat. These considerations were taken into account in the design of predictive modelling of raven distribution and breeding performance undertaken in subsequent chapters.

7. The statistical modelling of raven dispersion and breeding performance required measurements of many habitat parameters, at a fine spatial resolution, and over a wide geographical area. This was achieved by using satellite images of land cover and digital terrain modelling of land topography. A GIS was used to manage these and other spatial data, and provide a mechanism for extracting large quantities of summary information.. Land cover was mapped at a fine spatial resolution by production of a classified map derived from two satellite images acquired by the Landsat 5 thematic mapper. Initially, these were partially classified by unsupervised clustering algorithms. Final classification was derived by correspondence analysis of values on the partially classified image with values from vegetation maps which were made available to this project. Measures of topography were derived by digital terrain modelling of contours digitised from published maps. From this model separate maps were derived of altitude, slope, aspect and land surface ruggedness, each of which was also classified into separate categorical maps. Potential human disturbance was included by digitising roads and buildings from published maps.

8. Theoretical problems concerning statistical modelling of habitat data and animal dispersion are raised. These primarily involve the conflicting demands of the best size of area in which to measure habitat and the size of the area used to map presence or absence of the animal. These problems are particularly severe when, as is the case with ravens, habitat needs to be measured in areas much smaller than home range size. These problems were overcome by adopting a two tiered approach. First, a minimum Grid Unit of Location

(GUL = 500m x 500m) was adopted which was much smaller than home range size: thus habitat surrounding a hypothetical home range around the centre point within this cell was assumed to be representative of that surrounding any point in the cell. Secondly, habitat was measured in large regions (up to 100km^2) around each of these GULs. A second GIS was established to map the results of predictive models, and to perform deductive modelling based on this information.

9. Throughout, the emphasis was placed on 1) predictive modelling and 2) using these predictions to explain observed gaps in the distribution of breeding pairs. A first step was to identify these gaps in parts of the study area where the complete distribution of ravens was known. As ravens are territorial many locations could be eliminated simply because they were too close to an existing pair. I identified gaps in the observed distribution of breeding pairs by eliminating GULs which fell within a radius of regional mean nearest neighbour distance around existing pairs in 1990. There were many vacant GULs in this year, and most of these tended to occur in large clumps. These clumps were distributed across the study areas.

10. The availability of nest-sites can limit distribution in many raptors, however this was unlikely to be the case for ravens as they will resort to a very wide variety of sites. However, nest-site quality may have affected breeding performance and was therefore an important consideration in modelling. Detailed measurements of nest-sites were made at a large sample of sites but no relationship between these measurements and breeding performance could be detected. Thus nest site quality did not need to be considered in modelling, merely presence or absence of a platform suitable for the placement of a nest. Many GULs in gaps (47%) could be reliably excluded because they did not meet this condition, by examination of symbols given on Ordinance Survey maps. However, the distribution of those which remained led to the conclusion that lack of potential nest-sites was not responsible for the absence of ravens in many GULs.

11. Principal components analysis was used to reduce a large number of habitat variables thought to influence suitability for occupation by ravens (forestry and agriculturally improved land) into a smaller number of orthogonal components of variance. The data were structured in a way which allowed variance in

distribution of these land covers around the nest to be included. A novel use of GIS permitted many thousands of cases to be considered simultaneously in principal component space and identified as being within or outside the multi-dimensional limits described by occupied sites. GULs which were within these limits in principal component space were classed as suitable for occupation by ravens. Of vacant GULs with potential nest sites 43% were excluded on this basis. Most GULs within large forestry blocks were classed as unsuitable, however many of those along forestry borders of where forestry was fragmented were classed as suitable.

12. Human disturbance from roads and buildings did not influence suitability for occupation. Poor quality habitat produced by afforestation or agricultural improvement did not account for the observed gaps in raven distribution.

13. The modelling of suitability for occupancy took no account of the quality of semi-natural habitats remaining. As habitats which were important to the birds was unknown, evaluation of habitat quality to ravens was assessed predictive modelling of parameters of breeding performance using habitat variables. Logistic regression was used to derive robust models to predict clutch size and timing of breeding. Many vacant GULs predicted to be suitable for occupation were also predicted to be suitable for early breeding and large clutches.

14. It was concluded that neither shortage of nest-sites, human disturbance or unsuitable habitat could account for observed gaps in raven distribution. Other factors, such as the distribution of eagles, accounted for very few of the gaps. Thus the raven population in mid-Argyll was estimated to be only 48% of the maximum which could have been accommodated. Poor recruitment was implicated as the cause. It was concluded that in this area the present degree of afforestation is not limiting the raven population, but could set an upper limit on any increase in numbers.

15. The technology used in this thesis is likely to become more widely used in the future but is at present a fledgling field for ecologists. I have shown that this technology is now within reach of non-specialists and

can be combined with stochastic modelling. This may provide new insights into the spatial relationship between a species and its environment which can complement traditional mechanistic approaches.

CHAPTER 1. INTRODUCTION

The British uplands support a high density assemblage of carrion-eating/predatory birds regarded to be of international significance (Ratcliffe and Thompson, 1988). This assemblage consists of five species: golden eagle (*Aquila chrysaetos*), raven (*Corvus corax*), red kite (*Milvus milvus*), buzzard (*Buteo buteo*) and carrion/hooded crow (*Corvus corone*). The first three species, and in some upland habitats also buzzards and crows, are considered to be dependent on carrion as a food source, at least at certain times of the year (Watson *et al*, 1987, 1992; Ratcliffe, 1962, 1990; Davies and Davis, 1973; Hewson, 1981, Houston, 1977). In most areas occupied by these birds dead sheep (*Ovis aries*) and red deer (*Cervus elephus*) are the principal sources of carrion. There is a great deal of concern about the conservation needs of these birds, as well as other upland raptor species such as hen harrier (*Circus cyaneus*), merlin (*Falco colombarius*) and peregrine falcon (*Falco Peregrinus*) (e.g. Ratcliffe and Thompson, 1988; Ratcliffe, 1980, 1990a, in press). For the scavenging/predatory birds, however, the problem is complex because of the interplay between sheep and deer populations, these animals and their habitat, and habitat determination of mortality (and thus carrion supplies for the birds).

These birds require large areas of land for foraging, which are, to date, inadequately protected by site-based conservation methods alone (Thompson *et al.*, in press). As a first step towards better conservation of the species it is important to identify the relationship between land-use, habitat quality and the species ecology. This needs to be presented in a form that is of use in making strategic land-use decisions. From a conservation perspective it is important to be able to predict where numbers of birds will change in relation to land-use change; to identify features of land management that will enhance the survival of the birds and their productivity; and to facilitate better means of monitoring the birds and their habitat. Recent advances in information technology provide ecologists with new tools to address these issues. In this study this technology was used to investigate raven distribution and breeding performance in relation to habitat in mid-Argyll. The raven was chosen because it presents particular problems for conventional approaches to this problem and it is used as a model to explore ways of predicting bird distributions and breeding

performance from readily available habitat data. The methods developed in this study may also be useful for other species such as the golden eagle, which present even greater difficulties for field studies.

In this chapter, I outline the biology of the raven and the threats it faces in Britain from wide scale changes in traditional land-use. I then introduce new techniques available in information technology which not only aid in the process of modelling the influence of habitat on animals such as ravens, but which also meet the second requirement given above. This is followed by a description of the aims of this thesis.

BIOLOGY OF RAVENS

Territoriality and population density in Britain

The raven is the world's largest passerine, but exhibits many features in ecology and behaviour typically associated with raptors; indeed it is considered a 'functional raptor' in many community studies (e.g. White and Cade, 1971; Poole and Bromley, 1988). Ravens are large and can be long-lived, but Ratcliffe (1962), relying on identification of a few individuals by egg markings or unusual behaviour, found that few females remained on the same territory for over three years, and that in areas of heavy persecution there were changes in occupants every year. However, according to Heinrich (1990), ravens probably form lasting pair bonds, and once established in a territory usually occupy it for life. In the absence of any studies of individually marked breeding pairs these findings are conjectural. Territories are occupied year round, except for temporary absences in severe weather (Davis and Davis, 1986; Ratcliffe, 1990a), and tend to be regularly distributed throughout suitable habitats at densities that vary according to habitat and locality (Ratcliffe, 1962, 1990a). The birds typically defend with vigour a small area around the nest (the nesting territory), but not the much larger area (the home range) which they use for foraging (Ratcliffe, 1962). Home ranges have not been mapped in any British raven population, but their size is inferred from nesting density. Average nesting densities are reported from several areas in Great Britain and range from: low at 1-3 pairs/100km^2 in the Moffat Hills (Ratcliffe, 1962) and Perthshire (Stirling-Aird, 1988); moderate at 3.1-8 pairs/100km^2, in the West Denbeigh moors (Dare, 1986), Lake District (Ratcliffe,

1990a) and Orkney (Booth, 1979); to high at 8.1-14 pairs/100km², in Shetland (Ewins *et al.*, 1986), Snowdonia (Dare, 1986) and mid-Wales upland farmland (Newton *et al*, 1982). An exceptionally high density of breeding ravens of 21 pairs/100km² is reported from the mid-Wales uplands (Newton *et al*, 1982), and in the past very high 'linear' densities were recorded on sea-cliffs along the south-west of England (D. Nethersole-Thompson, in Ratcliffe, 1962).

Diet

All dietary studies to date have relied upon the analysis of remains in regurgitated pellets. This technique has acknowledged biases (reviewed in Marti, 1987) and food items which do not contain adequate roughage to occur frequently in pellets, such as invertebrates, may be under-represented. Studies of raven diet in different parts of their range have shown that an extremely wide variety of food may be taken: the raven is clearly omnivorous and able to adapt its diet to the available food supply. In the diet of most of their populations large mammal carrion often predominates (reviewed in Heinrich, 1990). In Britain, sheep carrion is prevalent in the diet of most populations studied (Ratcliffe,1962; Marquiss *et al*, 1978; Ewins *et al*, 1986). However, ravens inhabiting areas with few sheep carcasses available, for example Orkney, where beef cattle are the main agricultural produce, or areas that are well shepherded, are more dependent on rabbits (*Oryctolagus cuniculus*), many of which are taken as carrion (Marquiss and Booth, 1986). Road casualties may be important sources of carrion in some areas (Hope-Jones, 1980) and coastal pairs take a wide range of items from the littoral zone. Some pairs may specialise on locally abundant food sources such as eggs from seabird colonies (Ewins *et al*, 1986). Non- territorial birds make frequent use of human waste at rubbish tips and middens (Newton *et al*, 1982; Davis and Davis, 1986). In upland areas, sheep carrion is exploited more in winter and a greater variety of food (invertebrates, small mammals, lagomorphs) is taken in summer, probably reflecting their availability. Vegetable matter is often taken; in one population cereal grains were the principal pellet constituent (Engel and Young, 1989).

Habitat quality and ravens

Newton (1979) concluded that 'in any landscape, an upper limit to the number of established raptor pairs is set by food or nest sites, whichever is in shorter supply'. Home range size varies with food supply in many raptors (reviewed in Newton, 1979). The patterns underlying the great variation in raven breeding density in Britain are poorly understood, but are stated repeatedly as being related to the availability of sheep carrion (e.g. Newton *et al*, 1982; Ratcliffe, 1962; Ewins *et al*, 1986), although the availability of suitable nest sites seems to limit population density in some areas (Ratcliffe, 1962; Dare, 1986). Marquiss *et al* (1978) suggested that population density in the north of England and southern Scotland was lower at lower elevations and where land productivity was high, though this was probably due to a greater availability of sheep carrion on high ground with acid soils, rather than a more general relationship with the intrinsic productivity of the land.

Young ravens remain within their parents territory until autumn, after which they can disperse widely. During their first winter they join non-territorial flocks composed of immatures and adults (Heinrich, 1990), as also occurs in some other corvids, e.g. carrion/hooded crows (Charles, 1972, *in* Yom Tov, 1974) and magpies, *Pica pica* (Birkhead *et al*, 1986). Ravens reach sexual maturity at around 3-4 years of age (Heinrich,1990) but cannot breed until they either pair with a solitary territory holder, find an empty territory, or displace an existing territory holder. In each case, they must compete with other potential recruits to the breeding population.

A study of magpies showed that status in the non-breeding flock is strongly influenced by timing and distance of dispersal, with later or further dispersing birds obtaining only low ranks, and that variation in these factors may be related to food shortages in the natal territory (Eden, 1987). Richner (1989) found that natal (where birds were reared) habitat quality directly affected subsequent recruitment of carrion crows into the breeding population. Thus, in conjunction with the individual performance of breeding pairs, habitat quality may influence not only breeding density and performance but also the quality of offspring produced and their subsequent recruitment. Very few studies, however, have attempted to

identify the separate contributions of bird quality and territory quality to breeding performance. The highest quality birds should obtain the best territories, so the two will be highly correlated. However, in populations of a territorial species where there is a substantial non-breeding surplus population in which a social dominance structure exists, the new recruits should theoretically be the most dominant birds. If vacant territories are in very short supply, recruits should improve their inclusive fitness by accepting whichever becomes vacant regardless of habitat quality. This process has been shown in carrion crows (Charles, 1972, *in* Yom Tov, 1974; Richner, 1989). This interpretation is also supported by the findings of Goodburn (1991) who concluded that the relative contribution of adult quality and territory quality may vary within magpie populations dependent upon population density and turnover, and territory heterogeneity.

RAVENS AND THE UPLANDS

Distribution

The raven was once widespread throughout Britain but by 1900 had been all but exterminated from lowland regions, and even from some upland areas, by persecution in the interests of sheep and game management. It is now restricted largely to the wilder, coastal and upland regions in the north and west. In these areas raven populations remained unaffected by the activities of man, until recent decades, and were characterised by a remarkable stability in the distribution and density of breeding pairs (Ratcliffe, 1962, 1990a).

Around 30% of Britain's land surface area can be classed as upland in nature, which is typically defined as land above the 'upper limit of enclosed land' (Ratcliffe, 1977). Regional differences in this boundary are related principally to increasing oceanic influence from east to west, and decreasing temperature from south to north, such that there is a gradual altitudinal descent of life zones towards the north and west (Ratcliffe and Thompson, 1988; Thompson and Brown, 1992). Anthropogenic influences, notably forest clearance and creation of grazing range for sheep, have severely reduced the occurrence of natural communities, and below the tree line almost all habitats are influenced significantly by man, directly or

indirectly (Miles, 1987; Birks, 1988). These influences were significant by 3000 b.p. and have continued to the present day, producing a unique and highly varied landscape dominated by semi-natural or man-made vegetation communities. In turn these areas support an avian community with an unusual mixture of species (Ratcliffe and Thompson, 1988). Ratcliffe (1990b) considered the raven a key species of upland sheepwalk, acting as a 'wildlife barometer' for other animals and plants also associated with this habitat.

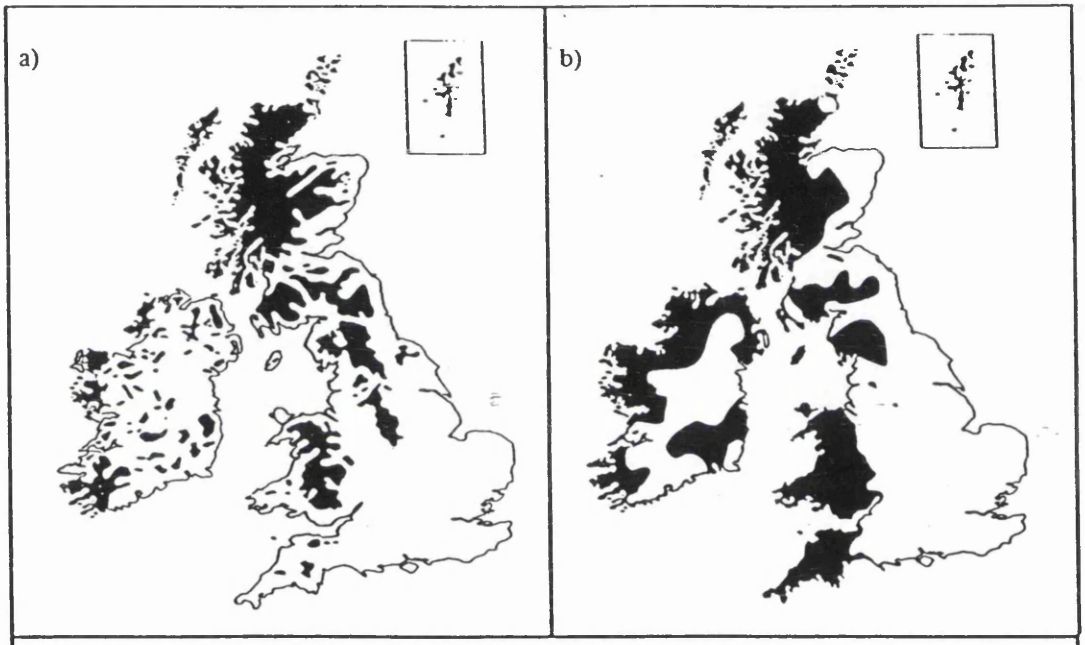

Figure 1. (a) The extent of Britain's uplands and (b) the distribution of ravens in the British Isles 1968-72
a) adapted from Ratcliffe, 1990a; b) adapted from Sharrock, 1976.

Land-use changes in the uplands

The uplands are undergoing a period of rapid change. Changes due to agriculture and afforestation far outweigh all other land-use activities in their effect on the upland bird fauna (Ratcliffe, 1990a), and have had a dramatic influence on ravens in some regions. The two main changes which have occurred are i) the loss of semi-natural upland vegetation through agricultural improvement, and ii) the gross loss of open upland habitats to coniferous forestry (Bunce and Barr, 1988). In the first case, so called 'improvement' of marginal hill-ground by drainage, application of fertiliser and reseeding results in habitats which are unlikely to have retained their original wildlife (Bibby, 1988) and so may result in a reduction in potential

prey for ravens. In the second case, changes in land-use due to the wide-scale planting of exotic conifers in most upland areas during the last 40 years has had the most dramatic effect on populations of ravens. Blanket afforestation is probably responsible for declines throughout much of southern Scotland and northern England (Marquiss *et al*, 1978). Sheep are removed from the areas to be planted, thus removing this source of carrion, and afforested land is much less suitable for hunting by scavenging birds (Thompson *et al*, 1988), at least after it reaches the thicket stage at seven to ten years. In the short term after planting, before growing conifers form a canopy, the reduction in sheep and deer grazing, caused by plantations being fenced-off, results in a more luxuriant growth of hill vegetation with more abundant prey for predators. However, in the long term, land placed under conifers is effectively removed as a foraging area for ravens.

Two large-scale studies have been made of the effects of habitat loss due to afforestation on British raven populations. Marquiss *et al.* (1978) produced good evidence that a 45% decline in the number of breeding ravens in the north of England and southern Scotland, monitored from 1946 to 1975, was due to the influence of afforestation. Not only did pairs desert territories when these were afforested, but breeding performance was reduced in proportion to the amount of the area around the nest site placed under trees. In mid-Wales, however, Newton *et al.* (1982) did not find any of these effects on ravens, even though many individual territories were subject to the same amount of afforestation as in the first study. An explanation for these differences (reviewed in Avery and Leslie, 1990) was that ravens in Wales were better able to tolerate habitat loss due to afforestation because they had better food supplies (in particular sheep carrion), which did not fall below threshold levels for occupancy and breeding success even when habitat loss was substantial. This answer is obviously incomplete as it does not explain why pairs in Wales occupied ground apparently in excess to requirements in the first place. It cannot be that the population had previously reached a behavioural limit to territory size above the potential carrying capacity of the land, as ravens in this part of Wales, though at the highest recorded density in Britain of up to 21 pairs/100km^2 (Davis and Davis, 1986), were at a population density far below the maximum recorded for

the species of 72.6 pairs/100km^2 in Idaho, USA (Kochert *et al.*, 1976, *in* Nogalez, 1990), or in Europe of 35 pairs/100km^2 in the Canary Islands (Nogalez, 1990).

Changes in sheep farming practices also appear to be influencing the success of raven populations, directly through the supply of sheep carrion, and indirectly through the impact of grazing pressure on upland vegetation and therefore on the abundance of live prey. Grazing pressure on upland vegetation has grown with increases in sheep numbers and stocking density throughout most of the uplands in the last 50 years (Sydes and Miller, 1988; Thompson *et al.*, in press). In Scotland, this has also been exacerbated by a doubling in numbers of red deer between the 1960s and 1989 (Red Deer Commission, 1989). Sheep grazing may affect prey availability by i) removal of considerable quantities of the primary production (Coulson, 1988) and ii) producing a change in vegetation from dwarf shrub to grasses with consequent reduction in the numbers and diversity of moorland fauna (Sydes and Miller, 1988; Usher and Thompson, in press). From a raven's perspective this reduction in potential prey may be compensated for by an increase in carrion availability, as traditional methods of sheep management result in a heavy mortality of ewes and lambs, and overstocking red deer results in increased natural mortality (Red Deer Commission, 1989). Raven density seems to be linked to the amount of sheep carrion available in many areas: in Snowdonia the raven population increased by 80% in the period between 1950-53 and 1978-85, apparently as a result of a substantial increase in sheep stocking rates (Dare, 1986; Ratcliffe, 1990a).

The increases in the numbers of sheep and deer on the hills may therefore have resulted in a much greater supply of carrion in some areas. However, improvements in sheep management, particularly over the last two decades, have led to a reduction in mortality. This may have more than counterbalanced the effect of greater numbers of sheep available to die, although figures to support this contention are not yet available. The apparent reduction in sheep carrion has been thought in part to be responsible for declines in raven populations in southern and central Scotland (Mearns, 1983; Mitchell, 1981). In addition, more effective culling of red deer being sought by the Red Deer Commission (1989), might reduce the number of red deer carcasses available in the future.

Scavengers, such as ravens and golden eagles, may be at high densities in some areas as a result of the copious supply of carrion, and a reduction of this supply may lead to a corresponding reduction in density unless alternative food sources can be found. However, a reduction in grazing pressure may give rise to higher densities of wild prey in more fertile areas where productivity of wildlife was kept artificially low (Watson *et al*, 1989). Watson *et al* (1992) found that nesting density of golden eagles in Scotland was higher where amounts of sheep and deer carrion were high, whereas breeding success was greater where live prey was more numerous.

MODELLING THE INFLUENCE OF HABITAT ON SPECIES DISTRIBUTION AND BREEDING PERFORMANCE

Avery and Leslie (1990) have pointed out that detailed studies from many different areas are necessary to fully assess the effects of land-use change on a birds , but that there are few species for which such studies have been carried out. For several distinct parts of Britain, data on raven distribution and breeding performance are available for many years, providing scope for more detailed analysis. However, attempts to explain differences in raven populations between areas, or changes over time, have been largely confined to the influence of afforestation and carrion availability. Such attempts are confounded by an almost complete ignorance of population-dynamics of ravens and their relationship with habitat in any region, as there are great practical difficulties in addressing such topics directly by field observations. A useful approach in the absence of such information is to infer relationships indirectly by comparison of dispersion and breeding performance of ravens across a range of environmental variables, both within and between populations.

In order to predict the effects of some change in environment on a species it is first necessary to define the relationship between that species and the present-day, measurable environment. The environment can be described as a spatial array of variables, most conveniently represented as a map of attributes either at a moment in time (e.g. a vegetation map), or summarising temporal effects in space (e.g. a map of climatic

zones). The temptation for many ecologists dealing with such spatial data is to produce large numbers of maps without having specific objectives, except as archive data. Although maps provide an efficient method of demonstrating distributions of phenomena in space, proof of causation or association remains an analytical problem (Howe, 1986). Until recently the difficulties in integrating different data sources without loss of spatial context have proved insurmountable. Recent advances in computerised information systems, of which Geographical Information Systems (GIS) are a part, coupled with the availability of powerful computer hardware, presents ecologists with an opportunity to tackle these issues. GIS are now providing not only the analytical tools necessary to deal with a wide range of environmental issues such as conservation management of resources (Haines-Young *et al*, 1990) but also provide a 'new approach to habitat definition and the study of [species] distributions' (Haslett, 1990). The integration of remotely sensed data, which can provide a wide spatial coverage at a finer resolution than could be feasibly collected in the field, with GIS is providing ecologists with fruitful new directions in which to explore the interaction of organisms and their environment. In addition, the results of modelling using GIS can be easily transferred to a planning environment, as the output may be cartographic, whether digital or paper. In Chapter 5 I introduce GIS and satellite remote sensing more fully and provide a detailed review of several studies which used this technology.

AIMS OF THIS STUDY

There are formidable practical difficulties encountered in conducting field research on a species such as the raven. It occurs at relatively low density in rugged terrain, reacts to humans at long distances, is difficult to catch, and tends to nest on high, overhanging cliffs. Many traditional approaches used to investigate the interaction of habitat and ecology in birds are untenable when applied to ravens in the period allocated for this work. Instead, a more extensive approach, investigating the relationship between breeding density, distribution of breeding pairs and breeding performance of ravens in relation to land-use forms the principal area of investigation in this thesis. This follows the example of previous studies of ravens (Marquiss *et al*, 1978; Newton *et al*, 1982) and other birds which present similar difficulties for field investigation such as golden eagles (Watson *et al.*, 1987, 1992). The present study, however, attempts

a more thorough investigation by making use of GIS and remotely sensed data, with the emphasis on predictive modelling. A large area of mid-Argyll in the west highlands of Scotland was chosen for this work both because of its wide range of habitats and land-use, as well as much probable variation in carrion availability. Supplementary data were obtained from mid-Wales which permitted a comparison of parameters of distribution and breeding performance between two populations of different density.

The study has three principal aims: 1) to compare differences in raven breeding density and productivity between mid-Argyll and mid-Wales; 2) for mid-Argyll to model individual territory location and breeding productivity in relation to measurable differences in the environment, using remotely sensed data and GIS; and, in so doing; 3) to develop methods of integrating stochastic and cartographic modelling of these ecological relationships, which may have general application to a range of species.

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CHAPTER 2. STUDY AREAS AND METHODS

Studies were conducted principally in mid-Argyll in 1989 to 1991. Funds were secured from the Nature Conservancy Council to employ Mr. A.C. Cross as a temporary field assistant, who collected raven nest history data in mid-Wales during the springs of 1989 and 1990.

STUDY AREAS

Location

Field studies of ravens in mid-Argyll were conducted in a large area (c6000km^2) chosen to include a wide variety of habitats and which also contained enough pairs of ravens in each broad habitat type for analysis. The area was bounded by Loch Lomond in the east and extended westwards to the west coast of Mull. The area extended south to the Cowal peninsula and north to a line roughly drawn between Crainlarich and Oban. Observations were also made by A. Knight and S. White of ravens breeding on Coll and Tiree to supplement information provided by me. The extent of the raven study area is illustrated in Figure 2.1. Most of this area was extensively searched during 1989 and on the basis of this work it was possible in 1990 to concentrate on five sub-areas (total area 1689 km^2) in which the raven distribution was well known and which differed in landscape and land cover (Figure 2.2). The boundaries of these sub-areas were defined as within a 5km buffer, i.e. beyond the mean nearest neighbour distance between sites, of an area in which all raven territories were known. Sub-areas were: Glens (283 km^2); Lorn (635 km^2); Cowal (129 km^2); Mull (552 km^2); and Tiree (90 km^2).

The study area in mid-Wales was the same inland area as that chosen by Newton *et al* (1982) for their study of ravens and buzzards . In 1986 a repeat census of ravens was made in this area (Cross and Davis, unpublished). Since then all raven nests in this area (expanded by 1989) have been monitored for ringing purposes. This area was again used for detailed studies in 1989 and 1990 (Figure 2.1). Information on additional pairs surrounding this area was collected from an area of some 1600km^2, and extended to the coast. As for sub-areas in mid-

Argyll the intensive study sub-area boundary was defined as within a buffer, in this case 3km, of the area in which all raven territories were known (587km^2).

Habitats

Habitats in mid-Argyll ranged from relatively high agricultural productivity coastal machair on Tiree, Coll and in a few places on the west coast of Mull, to barren high ground up to 1100m altitude on the mainland and inland Mull. The landscape reflected the underlying geology of granites, basalts and schists, and the action of glaciation: large U-shaped glens, separated by narrow ridges in the granitic and basaltic areas with more gently undulating ground in areas of schist. Fresh or salt water lochs were present in most glens. Cliffs were plentiful in many areas, especially the coasts. With the exception of the coastal machair strip most of the area was underlain with peat or acidic soils. The land capability for agriculture for this area was almost all graded as suitable only for rough grazings or as very limited agricultural value (Macaulay Institute for Soil Research, 1981) and base poor vegetation predominated: *Molinia caerulia* and *Nardus stricta* dominated sheep walk with extensive areas of poor condition dwarf-shrub heath. Much of the area was given over to sheep farming. There was limited intensive agricultural 'improvement' (drainage, fertilising and reseeding to create pasture) in low lying coastal areas and along valley floors, but many inbye areas had been subject to drainage. Cattle rearing predominated on Tiree but was not widespread across the rest of the area and was limited to some low lying farms. Several large estates in the area maintained large herds of red deer, with keepers and stalkers. There was little management of moorlands for grouse, and in most of these areas grouse stocks have declined over the years (Watson, *et al.*, 1987).

In mid-Wales the underlying rocks were predominantly Silurian shales. The area comprised many open areas of flat or gently rolling upland (maximum altitude 735m) separated by wide valleys, dominated by *Molinia* or *Nardus/Festuca* grasslands. Sessile oak (*Quercus petraea*) and mixed deciduous woodlands were more prevalent than in mid-Argyll. There were few natural water bodies, but several valleys had been flooded to make large reservoirs. Agricultural practices were similar to mid-Argyll with most land given over to hill-sheep farming. Many inbye and lowland areas had been subjected to agricultural 'improvement'. Red deer were

absent, and there was very limited management for red grouse (*Lagopus lagopus*). Large cliffs were rare compared with mid-Argyll.

Commercial forestry was widespread in both areas, ranging from small plantations of exotic conifers on farms, serving as shelter belts until harvesting, to much larger unbroken tracts of monoculture plantation, covering several square kilometres, operated by the Forestry Commission and several private companies. Argyll was one of the first upland areas to commence commercial forestry and some forests were on their second or third rotation. However in the last 10-20 years much new ground was planted and there were large areas of new-plant and pre-thicket forestry. Compared to the pattern of planting in the southern uplands of Scotland and northern Pennines of England, where huge tracts of unbroken monoculture stretch for many kilometres in any direction, continuous blocks of forestry were small in mid-Argyll and mid-Wales. This was presumably partly due to the rugged landscape (in Argyll), and the piecemeal fashion in which land had been given over to afforestation over the years.

Other land-uses were similar in both areas: a few small urban areas; occasional quarries; no heavy industry; no major fisheries and very little recreational disturbance away from major roads. Typical scenery from study areas are shown in Figures 2.3 to 2.9.

Persecution of ravens

In mid-Argyll, persecution of 'pest' species by keepers and farmers appeared to be solely concerned with controlling numbers of foxes (*Vulpes vulpes*) and crows and there was no evidence of direct interference with breeding ravens except at one site on Coll. The use of poison baits for 'pest' control, which has had a devastating effect on ravens in the eastern Highlands of Scotland and elsewhere (Weir, 1978), did not appear widespread, with only a handful of suspected incidents in the last decade in the area (M. Madders pers. comm.). In mid-Wales there was little keepering, but much persecution of crows and foxes by farmers. There has been evidence of deliberate destruction of raven nests, shooting of adults and illegal use of poisons on several farms. Overall I judge ravens to be more heavily persecuted in mid-Wales than mid-Argyll, but at a

low level compared with those in grouse and pheasant shooting areas of the country such as the English northern Pennines and in north-east Scotland.

Raven food supplies and competitors

In both areas there were sheep carrion available on the hills, and in mid-Argyll the additional supply of red deer carcasses. Other potential food supplies such as rabbits, small birds and mammals, invertebrates, fruiting plants, rubbish tips and middens occurred in both areas, but I have no information on relative abundance or availability. In mid-Argyll golden eagles were common but were absent from mid-Wales, however, in mid-Wales red kites were common but absent from mid-Argyll. Foxes were present throughout all areas with the exception of Mull, Tiree and Coll.

ITINERARY

The project began in October 1988. The first winter was concerned with identification of study areas, interviewing local naturalists for information on raven distribution, a literature review, and assessment of methods to measure the abundance of sheep and deer carrion. Fieldwork on ravens and trials of carrion counts extended from February to August, 1989. Winter 1989/1990 was devoted to the analysis of data and preliminary attempts to derive a satellite classification of land cover at the Institute for Terrestrial Ecology, Monks Wood. In 1990 studies of ravens were conducted from February to July. From August, 1990, effort was devoted to obtaining a satellite classification of land cover, at the British Geological Survey, Edinburgh, the compilation of a geographical information system (GIS) in the Department of Topographic Science, University of Glasgow, and writing programs for the extraction of data for analysis. This was completed in September, 1991. Short field excursions were made in the 1991 raven breeding season to provide data for the testing of predictions derived from data collected in 1989 and 1990. Extraction and analysis of data and modelling on the GIS took place from October, 1991 to June, 1992.

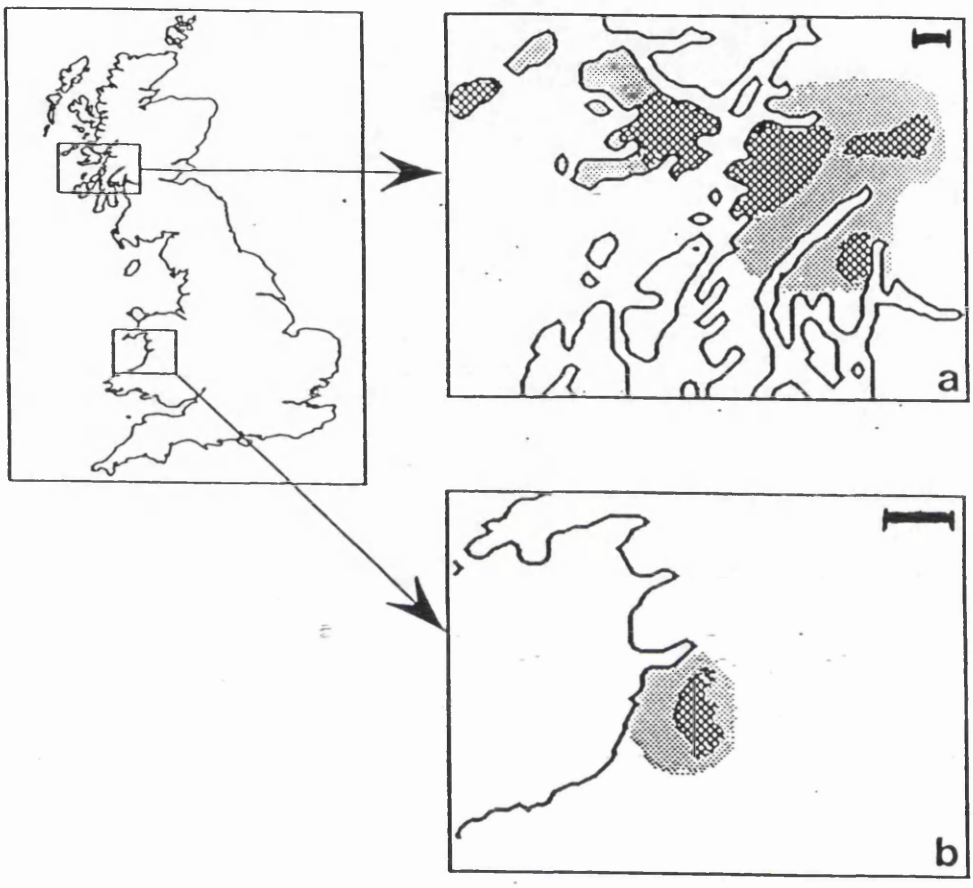

Figure 2.1. Location of study areas in a) mid-Argyll and b) mid-Wales.
light shading = total area in which ravens were observed
dark shading = sub-areas for which complete distribution of pairs were known for mid-Wales in 1989, and mid-Argyll in1990
= 10 km

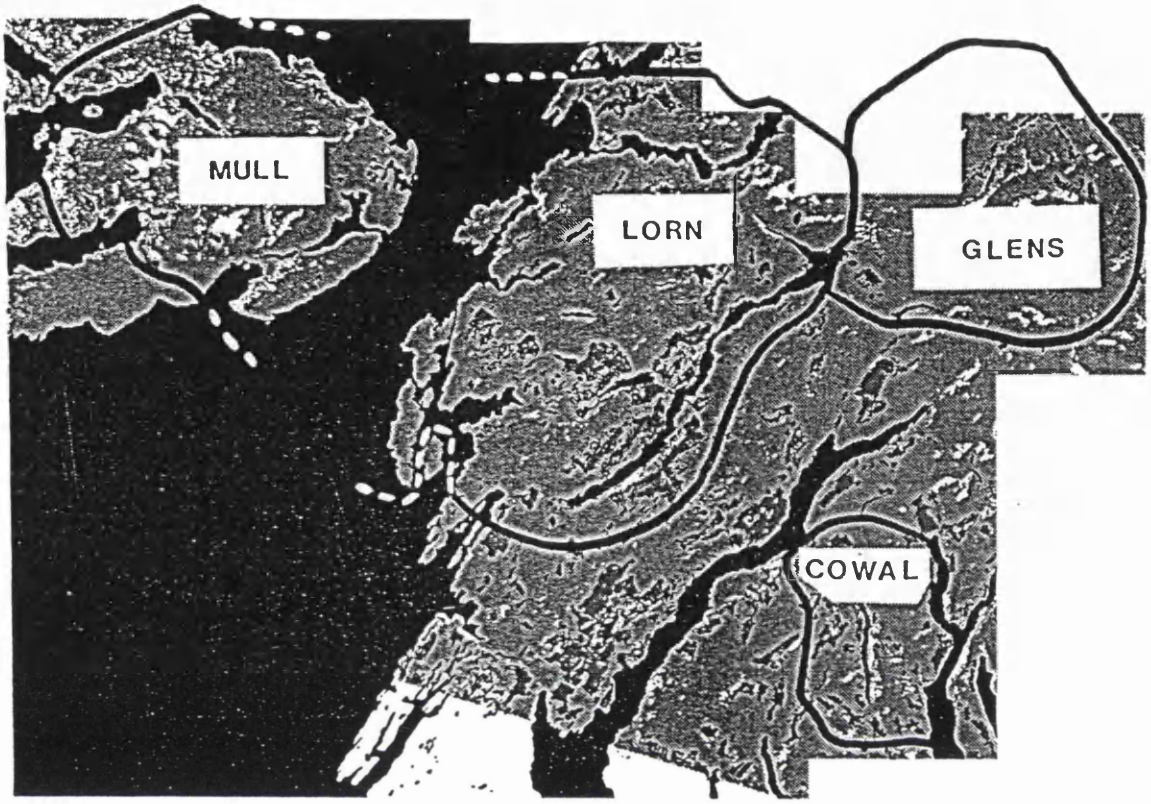

Figure 2.2 Locations of sub-areas in mid-Argyll for which complete raven distributions were known (solid black lines on land, dotted white at sea) laid over backdrop showing extent of area for which full GIS habitat data were aquired.

Figure 2.3. Glens sub-area, mid-Argyll.
Ben Lui viewed from Glen Lochy. Raven nest marked with an arrow. Note the extensive afforestation of the lower slopes.

Figure 2.4. Lorn sub-area, mid-Argyll.
Inland sheepwalk. Raven nest-site in deep gully marked with an arrow.

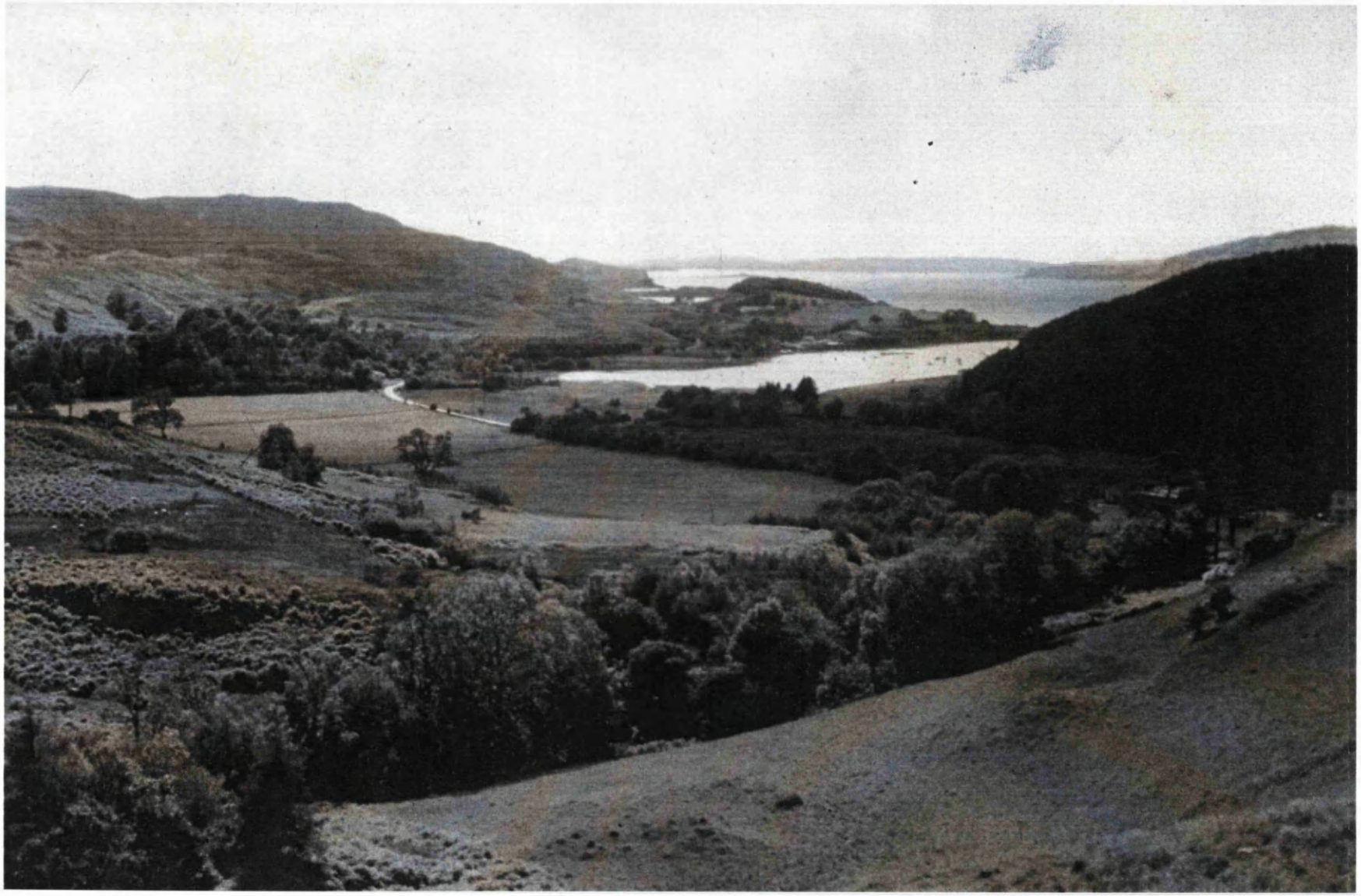

Figure 2.5. Lorn sub-area, mid-Argyll.
Coastal strip at the head of Loch Melfort. Tall cliffs were common on headlands.

Figure 2.6.Cowal sub-area, mid-Argyll.
Heavily afforested hills surrounding Lock Eck. Raven nest-sites (separate pairs) marked with arrows. Note author abseilling to nest in bottom left of picture.

Figure 2.7.Mull sub-area, mid-Argyll.
Coast along the Laggan peninsular, south Mull. Raven nest sites (separate pairs) marked with arrows.

Figure 2.8. Mull sub-area, mid-Argyll.
Barran inland deer forest dominated by *Molinea* with very poor quality dwarf shrubs.

Figure 2.9. Mid-Wales uplands.
Typical scenery with valley cutting through upland sheepwalk, and hanging oak woodland on steep valley sides.

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CHAPTER 3. ESTIMATING TIMING OF BREEDING OF RAVENS USING EGG AND CHICK MEASUREMENTS AND FIELD OBSERVATIONS.

INTRODUCTION

Timing of breeding is an important aspect of breeding performance (e.g. Lack, 1968) and in the context of this study was of interest because it may be influenced by land use (e.g. Marquiss *et al.*, 1978). Timing of laying is governed by stimulation of gonadal development with increasing daylength (Lofts and Murton, 1968), but may also be strongly influenced by food supply (Dijkstra *et al.*, 1982; Korpimäki, 1987; Daan *et al.*, 1989). As ravens, on average, breed earlier in the year than any other British bird with the possible exception of crossbills (*Loxia* spp.), variation in the timing of breeding may be an indication of late winter food conditions.

Although timing of breeding can be measured directly at the nest, for instance by observing laying, hatching or fledging, this usually requires several visits. In this study it was difficult to make repeat visits to sites, especially those in mid-Argyll, due to their remoteness and difficulty of access (see Chapters 4 and 8). However, using measurements from a known-age sample of egg or chick measurements it is often possible to produce species-specific formulae to estimate the age of clutches or broods at other nests of unknown age where measurements have also been made on a single visit.

Avian eggs lose weight at a fairly constant rate as incubation proceeds due to water loss through transpiration (Drent, 1970). Westerskov (1950) proposed a method of estimating the stage of incubation based on the negative correlation between time incubated and density in eggs of known age, and this has since been applied to many species (e.g. Furness and Furness, 1981; Green, 1984; Galbraith and Green, 1985). Similarly, the growth curves of morphometric features of chicks may be used as a basis for prediction of age. Predictions should not be based on chick weight as this varies with the amount of food in the digestive tract (Bechard *et al*, 1985) and is known to co-vary with environmental factors, such as food supply, to a greater degree than other morphometric measures (Moss, 1979). Growth rates of feathers

have been widely used to predict the age of nestling raptors (e.g. Peterson and Thompson, 1977; Bechard *et al*, 1985). However, studies have found that in times of food shortage, bone growth may be continued at the expense of feather growth, e.g. sparrowhawks *Accipiter nisus* (Moss, 1979), and measurement of tarsus or skull may therefore show less variance with age.

In this chapter I devise methods to determine the date of first laying which use measurements of eggs and chicks made at the nest. Where nest visits were not possible, as was the case for many sites in mid-Argyll, estimates of chick age were made from field observations using criteria given in Davis and Davis (1986), see page 48.

METHODS

Ageing clutches

When a clutch was located, clutch size was recorded and each egg numbered with an indelible marker pen. Each egg was weighed to the nearest 0.5g with a Pesola balance, and length and breadth at the widest point were measured to the nearest 0.1mm with callipers. Where possible, repeat visits were made at approximately weekly intervals and the identity and weight of surviving eggs was recorded. Clutches were considered to be complete only if incubation had commenced.

Where laying or hatching was observed, the date of first incubation was calculated by assuming that ravens lay eggs at approximately daily intervals (Hollyoak, 1967; Stiehl, 1985), begin incubating with the penultimate egg, and that first hatching takes place 21 days after the start of incubation (Davis and Davis, 1986).

For each egg an index of volume was calculated as length x $(\text{breadth})^2$. An egg density index was calculated for each weighing of an egg by dividing egg weight by egg volume index:

$$\text{Egg density index} = \text{weight}/(\text{length} \times (\text{breadth})^2)$$

A mean egg density index was calculated as:

$$\text{mean egg density index} = \frac{\Sigma \text{egg\_density\_index}}{\text{clutch\_size}}$$

For known age clutches a linear regression was performed between number of days incubated (the dependent variable) and mean egg density index (the independent variable). Repeat measurements of clutches at least seven days apart were treated as independent samples. 95% confidence intervals for a range of individual estimates were calculated to investigate the usefulness of the regression equation to predict the number of days which clutches of unknown age had been incubated.

Ageing broods using measurements of chicks.

Where access to the nest was possible the number of surviving chicks was recorded, and the following measurements taken of each chick, on each visit:

Combined head and bill length: with callipers to the nearest 1mm from the back of the skull to the tip of the bill.

Tarsus length: with callipers to the nearest 1mm from the notch in the ankle to the distal end of the metatarsals with the toes bent downwards at an angle of 90°.

Longest primary length: with a straight end ruler to the nearest 1mm from the base of the feather to the tip. Primary feathers did no begin to emerge until the second week after hatching. The longest primary was always either *p5* or *p6* (numbered according to Ginn and Melville, 1983).

Chicks were not individually marked until old enough to be fitted with individually numbered metal leg rings supplied by the British Trust for Ornithology.

Where possible the age of broods was calculated from observations of hatching or laying. Brood mean values for each measurement were calculated by summing the values from each chick and dividing by current brood size. Repeat measurements of broods at least seven days apart were treated as independent samples. Each morphometric measurement was in turn plotted as an independent variable against age as

the dependent variable and in each case a linear regression line fitted to the data. To examine the precision with which age could be predicted from each morphometric measure 95% confidence intervals for a range of individual estimates were calculated. The regression formula was used to age all other broods of unknown age where measurements were available, including repeat measures of the same brood. The estimated age of the brood at each visit was subtracted from the date of the visit, which was recorded as number of days since 31st January in each year. Estimated date of first laying was calculated as hatching date minus 21 days (incubation period) minus clutch size-2 (laying period). These were converted to week of first laying, classified in seven day intervals beginning on February 1st each year.

Ageing broods by field observations.

Davis and Davis (1986) record that most ravens in mid-Wales in 1975-80 fledged at about 45 days. In mid-Argyll, where in 1990 access to nests was rarely attempted, broods were aged to the nearest week from observations of fledging, using criteria given in Davis and Davis (1986), and from observations of known age broods. Chicks were often observed out of the nest but unable to fly properly and these were aged as six weeks old; weakly flying immediately around nest, seven weeks old; stronger flying young but still near nest, eight weeks old. Several repeat visits were often necessary to observe fledging, and the estimate of brood age was usually made on a series of such observations. The estimated hatching date was calculated as date observed fledging minus 45 days. These were converted to week of first laying using the same calculation as for estimates based on chick measurements. Ageing broods by field observations alone was not undertaken in mid-Wales. Estimates of chick age from field observations were retrospectively compared with estimates based upon chick morphometrics at four sites where both data were collected. Obviously laying dates of unsuccessful pairs or at sites where fledging was not observed could not be determined in the field using this method.

Estimating brood age by condition of the nest.

To obtain an estimate of laying date at sites where fledging did not occur or was missed, I used field records of nest condition. Adult ravens do not defecate on the nest, but chicks do. Only when they reach a

certain size are they able to defecate over the edge enabling splashings to be seen on the nest. By fledging the nest is trampled flat and is very soiled. Records of nest condition were made in mid-Argyll only. I scored splashings as: 1) absent; 2) present but in small quantities on the edge of the nest; 3) nest soiled and flattened. These were compared with ages estimated by other methods.

Analysis.

In all statistical tests a level of significance of $\alpha = 0.05$ was used, with two-tailed probabilities. Details of statistical tests used are given with the results. All tests were performed using SPSS/PC+4.0 (Norušis, 1990).

RESULTS

Estimation of laying date from mean egg density index

Eggs were measured at 17 nests where laying or hatching was also observed. Four clutches were measured once only, seven twice, and six three times, giving a total of 36 measurements. Individual egg density indices declined steadily during incubation (Fig. 3.1), with a sharper decline just before hatching which may be due to rapid water loss once the shell membrane had been pierced. Only clutches incubated for less than 20 days ($n = 30$) were included in subsequent regression analyses.

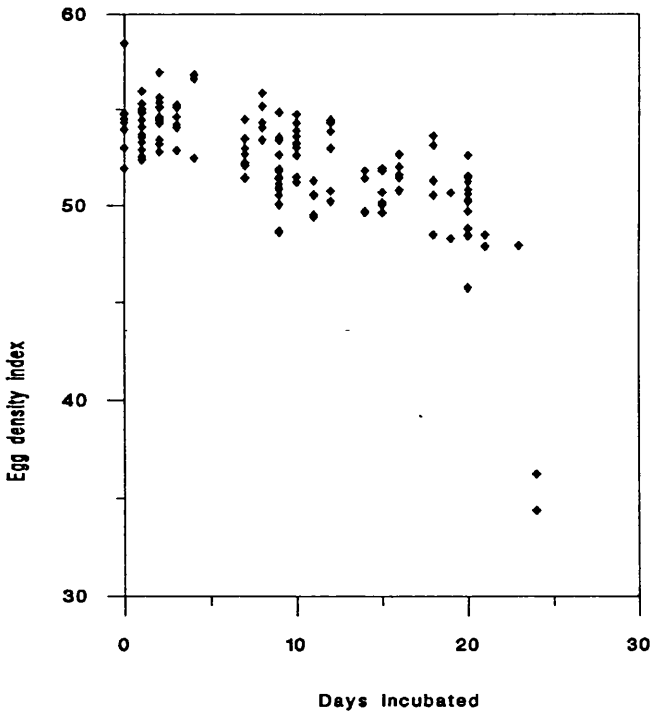

Fig. 3.1. Egg density index versus days incubated.
Egg density index = weight/(length x (breadth)^2)

A regression of days incubated against mean egg density index produced the following equation:

Days incubated = -2.83 (mean egg density index) +157.00

($p < 0.001$; r^2=0.63; s.e. of estimate = 4.18).

95% confidence limits of individual estimates were calculated for a range of mean egg density index values, and gave a range of +/- 14.11-14.12 days (Figure 3.2). The error may have arisen due to the asynchronous development of eggs within a clutch, but no improvement in 95% confidence limits of individual estimates was made by using a regression based solely on the least dense egg in a clutch, though the strength of the regression was slightly improved ($p < 0.001$; r^2=0.72; s.e. of estimate = 3.72) The error in estimating age from egg or clutch weight loss was considered unacceptably large and this method was not used to estimate first laying date.

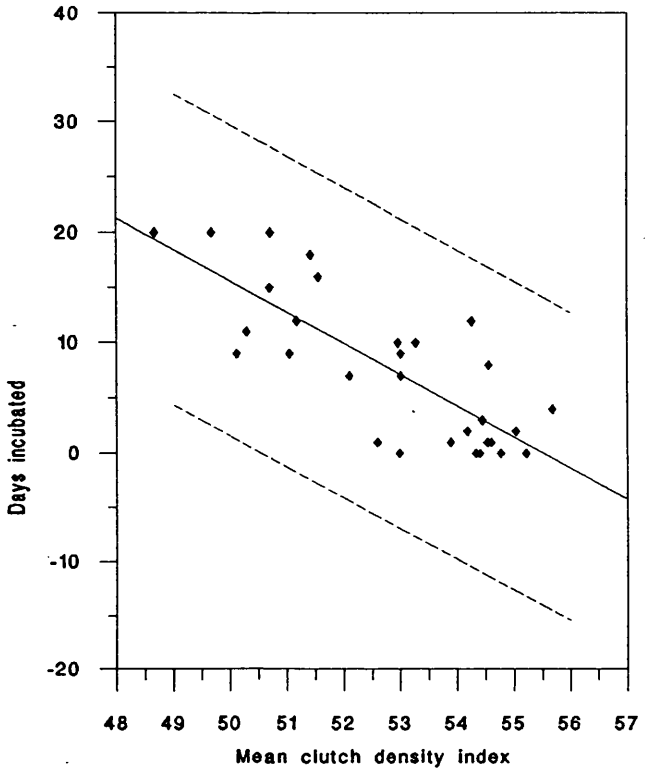

Fig. 3.2. Linear regression of days incubated versus mean egg density index
solid line: days = 157.00 + dens (-2.83); r^2=0.63, $p < 0.001$
dashed line: 95% confidence interval of individual estimates.

Estimation of hatch date from chick measurements

Measurements were made of 17 known age broods. One brood was measured once, 11 twice, and five three times, giving a total of 38 measurements. Growth of morphometric features followed a typical sigmoidal curve against age with the exception of primary feathers which were still growing at fledging (Fig. 3.3). Ageing chicks by eye prior to the emergence of primary feathers, is straightforward at least to the precision required here. The difficulty lies towards the end of fledging, and it is during this period that mathematical estimation would be most useful. As both tarsus and 'head and bill' had clearly reached asymptotic growth points before fledging (c45 days), these variables were discarded in favour of primary feather measurements.

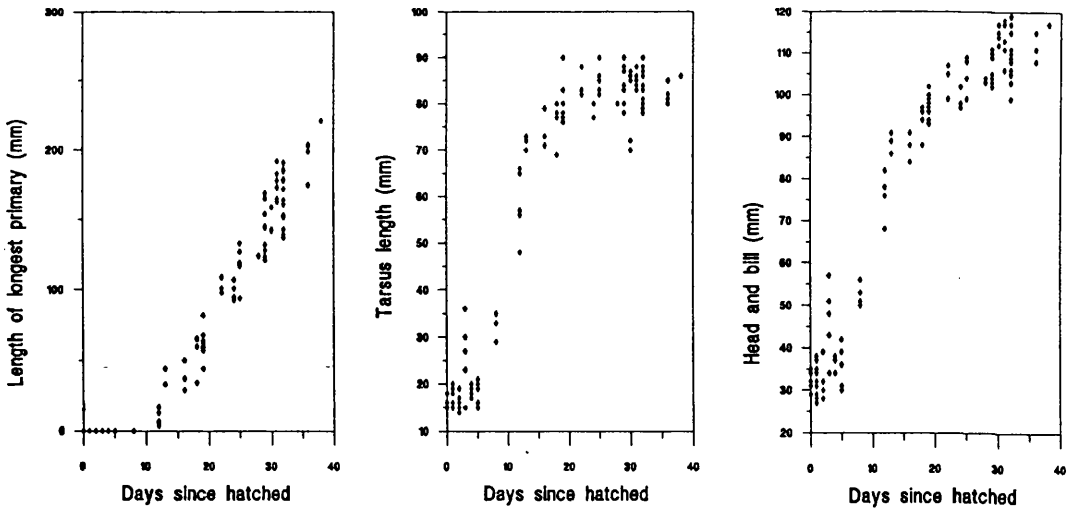

Fig. 3.3. Growth of longest primary feather, tarsus, and head plus bill length in nestling ravens.
X-axis: days since first chick in brood hatched
Y axis: morphometric measures are from individual chicks.

The regression of age versus brood mean longest primary length (BMLP), excluding BMLP values of zero, produced lowest values for the family of 95% confidence intervals of individual estimates (range +/- 2.81 to 2.98 days)(Figure 3.4):

$$\text{Days since hatch} = 0.12\ (\text{BMLP}) + 11.15$$

$$(p < 0.001;\ r^2 = 0.97;\ \text{S.E. of estimate} = 1.36).$$

This equation was used to estimate days since hatching for broods of unknown age. The mean value of estimates for a brood was taken where repeat measurements of a brood where BMLP > 0 were available. Chicks did not begin to grow measurable primary feathers until 11 days after hatching. Broods with no measurable primaries were, for the purpose of subsequent analyses, aged in the field to be in their first or second week since first hatching depending on size, but only one brood was aged on this criterion without further refinement from later measurements.

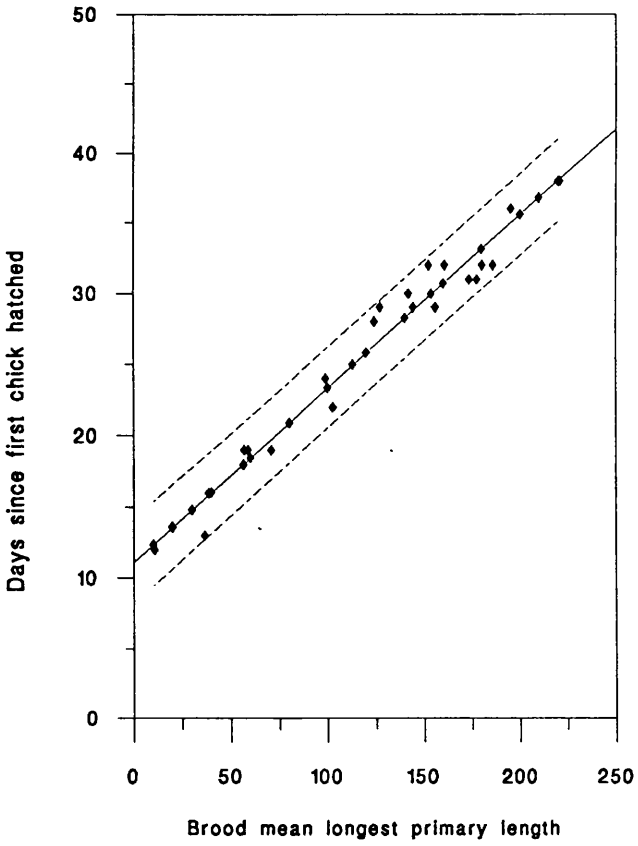

Fig. 3.4. **Linear regression of age against BMLP.**
BMLP = mean length of longest primary feather for each chick in the brood.
solid line: Age = (0.12)BMLP + 11.5 ($p < 0.001$; $r^2=0.97$).
dashed line: 95% confidence interval of individual estimates
as primary feathers did not begin to emerge before c11 days after hatching, chicks younger than this could not be aged by this method.

Calibration of field estimations

A comparison of first laying date estimated from field observations and derived from measurement of BMLP (retrospectively calculated after the field season) was possible at only four sites. The identical week of first laying was derived by both methods in three cases, whilst in the fourth the prediction from BMLP fell two days after the end of the designated week number assigned from field estimates.

Estimation of brood age by condition of the nest.

Nest fouling increased with increased stage of development, see Table 3.1. Score 1 was associated with eggs and young chicks under two weeks old; score 2 was associated with young chicks aged two to three

weeks after hatching; and score 3 was associated with chicks aged four weeks or greater. Whilst these estimates were useful in evaluating the developmental stage at which nest failures occurred (see Chapter 4) they were not precise enough for inclusion in further analysis.

weeks after hatching	nest condition score		
	1	2	3
0 (eggs)	9	0	0
1	2	0	0
2	1	2	1
3	0	2	2
4	0	0	4

Table 3.1. Nest condition score and age of nestlings.
score 1 = faecal splashing absent
score 2 = small quantity of faecal splashing on edge of nest
score 3 = nest soiled with faeces and flattened

DISCUSSION

The formula to estimate first laying date from calculated values of egg density did not permit estimates to be made within useful confidence intervals. This was probably due to a series of cumulative errors: using a constant for laying and incubation periods; using a constant in the formula for egg volume and taking no account of differences in egg shape; and assuming a constant decrease in density throughout incubation for each egg. Davis and Davis (1986) found incubation periods to vary between 17 and 21 days at six raven nests where this was recorded, indicating considerable variation. Such differences may be related to micro-climate or habitat associated differences in the incubational behaviour of the adults. Galbraith and Green (1985) found significant differences in incubation periods of lapwings *Vanellus vanellus* in two different habitats. Väissanen *et al* (1972) found significant, wader species-specific variations in egg shape of individual females, between clutches from the same female, and within a clutch. Raven eggs were

noticeably variable in shape between clutches from different hens. There is evidence that embryos of some species, where incubation does not commence simultaneously, can alter their rate of development to result in a more synchronised hatching of the brood, for example buzzards (Brown, 1976). Clutch size, nest construction and position in the nest can also greatly effect the thermal conditions of the egg and subsequent development time (Tullet, 1985). The additional field measurements required to correct these errors, such as determining the actual volume of eggs in the field (Thomas and Lumsden, 1981), would be impractical for ravens.

The date of first laying, to the nearest week, is most easily determined by the calculation using the mean value for the brood of the length of the longest primary feather on each chick (BMLP) if access to the nest can be made. This is recorded during one visit to the nest, and could easily be taken during the process of ringing nestlings undertaken in many localities. Using a mean value for the brood does not require knowledge of hatch order, and taking the longest primary of each chick rather than counting to a specific primary feather considerably reduces handling time. This is an important consideration when taking measurements in difficult circumstances at the nest. If BMLP cannot be measured, apparently reliable estimates of first laying date can be obtained from field observations. However, this usually requires repeat visits to a site to observe development at a crucial stage, an observer experienced with raven chick development, and may be impractical in large or dispersed populations, or where time for fieldwork is limited. Estimation of stage of development from soiling of the nest is a more subjective and less precise method than that based on chick measurements, but can be useful for determining if young have reached at least four weeks old. Davis and Davis (1986) reported that partial or complete brood loss after raven chicks reach three weeks old is extremely rare. Therefore nest condition is a useful indicator of successful breeding in the absence of direct observations.

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CHAPTER 4. REGIONAL DIFFERENCES IN RAVEN BREEDING DENSITY AND PERFORMANCE WITHIN BRITAIN

INTRODUCTION.

In this chapter I examine regional differences in raven density, distribution, breeding performance and size of the non-territorial population: first between mid-Argyll and mid-Wales using the detailed and compatible data acquired during this study (Part I); and then for all regions in the British Isles for which published information is available (Part II). I use these comparisons to draw conclusions about raven population dynamics and discuss the implications for studies of habitat requirements and habitat change in light of these.

Background: raven breeding biology.

Nest sites are traditional, although sometimes two or three alternative nest sites may be used within a territory in different years. The birds defend a small area around the nest against intrusions from con-specifics and potential competitors for nest sites or predators (such as golden eagle, peregrine falcon, *Falco peregrinus*, and buzzard) but not the much larger area used for foraging, outside which they do not usually stray (Ratcliffe, 1962). This type of territorial defence is common in many raptors; the wide area in which they range is termed by Newton (1979) the 'home range' and the heavily defended area the 'nesting territory'. Ravens breed early in the year compared to most birds in Britain. This is thought to enable chick rearing to coincide with the peak availability of sheep carrion in early spring (Ratcliffe, 1962; Newton *et al*, 1982). Raven clutch size is variable, usually from two to seven eggs. Larger clutches have been recorded but these were thought to be from more than one female (Allen and Naish, 1935). Incubation proceeds towards the end of laying and results in asynchronous hatching of young (Ratcliffe, 1962; Davis and Davis, 1986). Pairs may fail completely during incubation, but partial clutch losses are rare. Most chick mortality occurs in young nestlings and partial brood loss by death of the smallest chicks is common (Davis and Davis, 1986).

PART I. COMPARISON BETWEEN MID-ARGYLL AND MID-WALES.

METHODS

Field methods to determine occupancy and production of young.

Ravens were monitored in two areas, mid-Argyll and mid-Wales, during the breeding seasons of 1989 and 1990. In each area for at least one of the years, the complete distribution of pairs was known for substantial areas in each study site, and additional data were collected for pairs outside these areas.

In mid-Wales, the distribution of sites was well known from previous years, but gaps in this distribution were checked each year. In mid-Argyll, by contrast, few sites were documented at the start of the study (R. Broad, D.A. Ratcliffe, M. Madders, and A. Knight *pers comm.*), with most of those which were, being on Mull, Coll and Tiree. Consequently, much time in 1989 was spent identifying sites across the entire study area. The rugged nature of the terrain made searching difficult and time consuming; often many hours of walking would be required to reach a site. In 1990 I concentrated on pairs within five large sub-areas (Chapter 2), and searched these until I was confident that all pairs were located. Emphasis was then placed on determining breeding success and observations of fledging date for these pairs. Ravens nesting outwith these areas were studied opportunistically.

Identifying territories

Observations began at the beginning of February in each year. Territorial ravens are very demonstrative in the pre-nesting and nesting periods, and nests are usually easy to spot. It is unlikely that any successful pairs were missed. However, non-breeding and failed birds were less demonstrative by the end of March and were often absent from the nesting territory. In such cases, it was often possible to find old or abandoned nests by checking what looked to be suitable sites, and as most searches were completed in the pre-nesting and early incubation periods, the number of sites which had been abandoned and no nest located will be very small. Thick plantations of forestry presented great problems for foot searching, but by overlooking these areas for

adult activity and checking with local Forestry Commission stalkers it is unlikely that any pairs were missed. Searches of these same forests for buzzard nests undertaken by G.E. Austin later in the season did not uncover any new raven pairs. Most sites were checked several times, especially those apparently unoccupied.

Determining occupancy

In the absence of observations of breeding activity a pair was determined to be occupying a site if the birds exhibited territorial, mobbing or alarm behaviour at this location on more than two occasions. A site was determined to be unoccupied if records of previous occupation were available (the oldest records were from 1977 supplied by D.A. Ratcliffe), or an old abandoned nest was located (these regularly persist for many years, Ratcliffe, 1962), and no sign of ravens were found on at least two visits (each visit often spanned several hours) within a radius of half the distance to the next nearest raven territory. Most territories contained several alternative nest sites. In searching for and checking these it is unlikely that pairs occupying a new alternative site would have been missed.

Determining whether breeding was attempted and outcome.

Pairs were considered to have attempted breeding if a nest had been built, or an old nest rebuilt. In almost every case such observations were confirmed by observations of a female incubating, or, later, the soiling of nests by chicks. Breeding was 'successful' if at least one young was fledged. Earlier studies suggest that partial or complete brood loss after the chicks are three weeks old is extremely rare (Davis and Davis, 1986) and in this study all chicks over this age were considered to have fledged. In most cases success was determined by the presence of a fledged brood. On 10 occasions success or failure was not directly observed and I inferred it from the condition of the nest (see Chapter 3 for scoring procedure). I assumed that nests in condition 3 (indicating chicks aged four weeks or greater) had successfully fledged young. Nests which remained in condition 1 or 2 (chicks less than four weeks old) on repeat visits were assumed to have failed. This was usually confirmed by the activity of the adults. Throughout this chapter breeding status (yes, no or unknown) refers only to those territories which were occupied, and breeding success (yes, no or unknown) refers only to those territories where breeding had been attempted.

Davis and Davis (1986) reported only 9 repeat layings after nest failure out of 207 known first clutches laid in 4 year's observations. Unless several repeat visits were made throughout the season it was difficult to be sure that a late clutch or brood was a repeat attempt after a previous failure. There were three suspected relays in mid-Wales and none in mid-Argyll in 1989-90. In each case the timing of breeding was taken as that of the first attempt and success and fledged brood size from the final outcome.

Fledging or recently fledged ravens remain in close proximity to the nest site for some two weeks. Successful breeding was thus determined by a range of methods: 1) the condition of the nest only; 2) by observations of chicks still in the nest over three weeks old; or 3) by observations of newly fledged young in the vicinity of the nest-site in conjunction with the condition of the nest.

Measurement of nest contents.

Clutch size and the number of chicks hatched were determined by visiting the nest. In mid-Argyll this usually proved to be extremely difficult and dangerous. Most nests were on high cliffs and often under overhangs (see Chapter 8). To measure nest contents it usually required a substantial abseil, removal of eggs or chicks for processing on the ground, and a second abseil to replace them. The size of cliffs and friable nature of the rock in most areas made this task not without an element of risk and was inevitably time consuming. Consequently I made fewer nest inspections in 1989 than I had hoped and in 1990 relied almost entirely on visual observations of nest contents from a suitable vantage point or on an abseil past the nest. A plastic mirror mounted on a 1.5m pole was used to enable me to see into the deep and well lined nest cup where I could not see in directly. In mid-Wales, by contrast, most nests were accessible, permitting several visits to record progress.

Fledged brood size was determined by counts of chicks in the nest made during nest visits and subsequently aged to be 21 days old or older, and by counts of fledging chicks from suitable vantage points.

Measuring timing of breeding

Date of first laying was calculated from field observations of laying, hatching or fledging, or from calculations based on primary feather length of growing chicks, and recorded to the nearest 7 day interval beginning on February 1st each year (see Chapter 3).

Estimating the size of the non-territorial population during the breeding season.

At the outset of this study there was no clue to the size of the non-territorial population of ravens in mid-Argyll. I wished to determine the numbers of these birds in different areas, and their distribution and activities in relation to habitat and the distribution of breeding pairs. Two methods of recording field observations and observer effort in different habitats and locations were used, which made use of the considerable time spent travelling by foot and road which fieldwork required. These were devised and conducted jointly with G.E. Austin, who was concerned with buzzard activity. Davis and Davis (1986) and Newton *et al.* (1982) provided an estimate of the size of the non-breeding raven population in mid-Wales.

Hill Logs.

Habitat was classed into 10 categories (details are given in Austin, 1992), and during any walk a record was kept on a standard log-sheet of the time spent and distance travelled in each habitat. Distance was measured by a mechanical pedometer to the nearest 100m, and the identity of all 1km grid squares traversed on route were noted. A continuous record was kept of the weather. Simultaneous records mere made of all raptors and ravens observed, recording date, time and 100m grid reference observed, activity and habitat. In addition, the identity, location and condition of all large mammal carcasses discovered were also logged using these methods, but these data are not considered in this thesis (see Chapter 5). Routes and time spent in each area were determined by the routine of searching for and checking on raven and buzzard nests and were pooled from myself and G. Austin.

Road Logs.

All metalled roads across the entire study area were split into sections from 2 to 15 km in length, delimited by suitable road junctions, and assigned a unique code. A log was kept of the date, time of day, time spent

driving, and weather in each section. All observations of raptors and ravens were recorded along with 100m grid location, time, habitat, weather and bird activity. As for the Hill Log, routes and time spent in each section were determined by the routine of other studies and were pooled from myself and G. Austin.

Nearest neighbour distance

Nearest neighbour distance (NND) was used in comparisons of breeding density between mid-Argyll and mid-Wales, and to calculate dispersion statistics. Only occupied territories within intensive study areas (where I was confident that all occupied sites were known, see Chapter 2), and where nests were found, were considered. NND was measured by ruler on Ordinance Survey 1:50,000 maps of the study areas, from nest-site to nest-site, to the nearest 100m. Only one year was considered from each study area, that with the best coverage: for mid-Wales 1989, and mid-Argyll 1990.

Analysis

Each statistical test was performed under the null hypothesis that samples belonged to the same population, with a level of significance of $\alpha = 0.05$, with two-tailed probabilities, except for the multi-way frequency analyses of territory occupancy, breeding and success between years and areas described below. Details of statistical tests used are given with the results. All analyses were performed using SPSS/PC+4.0 (Norušis, 1990a).

Territory occupancy and breeding performance.

Occupancy, breeding attempt, and breeding success records were likely to be biased towards the positive as negative values were harder to determine and were probably classed as 'unknown' more frequently. The proportion of unknowns for each class was also likely to vary between study areas as topography and lower densities of birds made fieldwork more difficult in mid-Argyll, and between years in this area as there was no prior experience of sites to act as a guide in 1989. These inherent biases make it more likely that differences will be exaggerated between sites and/or years. Consequently, in multiway frequency analyses comparing these

parameters between sites and/or years the risk of committing a type 1 error (wrongly rejecting the null hypothesis) has been reduced by setting the threshold of rejection of null hypothesis to p = 0.01.

Density and dispersion.

The nearest neighbour statistic, *R*, was calculated as the ratio of the observed over expected NND (formulas from Selkirk, 1982):

$$R = NND_o / NND_e$$

where NND_o is the mean observed NND, and NND_e is the expected mean NND given by the following equation:

$$NND_e = \frac{1}{2\sqrt{\frac{n}{A}}}$$

where *n* is the number of points and *A* is the area.

95% confidence intervals for the R statistic were calculated using the formula

$$NND_e \pm 1.96 \times 0.261\sqrt{\frac{A}{n}}$$

For a random distribution of points, the value of *R* is one. Perfect clustering gives a value for *R* of zero and complete regularity approximately 2.15 (Selkirk, 1982) .

RESULTS

Density and dispersion.

The overall density of occupied raven territories in mid-Wales in 1989 was 11.1 pairs/100 km², and in mid-Argyll 3.6 pairs/100 km². The distribution of NNDs in each area is shown in Figure 4.1. There was a significant difference (t_{85}= 9.62, p<0.001) between the mean NND in mid-Wales (1.9km s.e.=0.08, n=66) and in mid-Argyll (3.6km, s.e.=0.17, n=58). The dispersion of sites in both areas showed some tendency towards

regularity. In mid-Wales (R_{Wales}= 1.27 ± 0.19) the lower value within 95% confidence limits was greater than one, whilst in mid-Argyll it equalled one (R_{Argyll} = 1.37 ± 0.37).

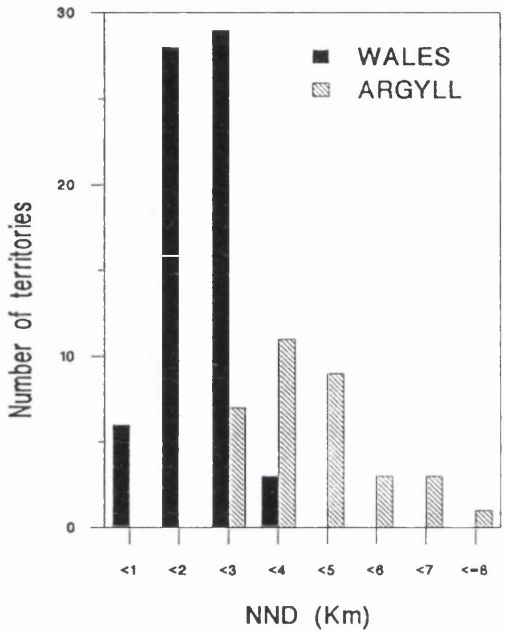

Figure 4.1. Nearest neighbour distance (NND) in mid-Wales (1989) and mid-Argyll (1990)

Differences in occupancy, breeding attempts and breeding success between years and sites

The numbers of occupied, breeding and successful territories for each year in mid-Argyll and mid-Wales are presented in Table 4.1. As some territories were checked in only one year, their occupancy remained unknown for the other year. The occupancy of territories in 1990 which were known to be occupied in 1989 is given in Table 4.2., to provide a sample unbiased by the knowledge of sites prior to 1989 available in mid-Wales.

In mid-Argyll in 1990, four breeding attempts were classed as successful and six unsuccessful on the basis of score of nest condition only. Using this score it was possible to retrospectively estimate the timing of failure at 11 breeding attempts in 1990 known to have failed. Eight of these failed on eggs or chicks under two weeks old, two failed on chicks aged two to three weeks old, and one failed on chicks aged four weeks old or greater. Thus most failures occurred on eggs or young chicks in mid-Argyll in 1990, and it was unlikely that one of the four nests classed as successful on the basis of nest condition alone had in fact failed at a late stage.

study site	year	occupied			breeding attempted			attempt successful		
		yes	no	?	yes	no	?	yes	no	?
mid-Argyll	1989	75	18	32	58	2	15	30	6	22
	1990	72	20	33	56	11	5	36	14	6
mid-Wales	1989	83	4	36	78	4	1	44	30	4
	1990	97	9	17	91	2	4	52	23	16

Table 4.1. Number of raven territories occupied, breeding and successful in 1989 and 1990 in mid-Argyll and mid-Wales.
? = unknown or uncertain
breeding records are for occupied sites only, and success for sites where breeding was attempted, in that year.

study site	occupied in 1990	deserted in 1990
mid-Argyll	44	10
mid-Wales	66	5

Table 4.2. Occupancy of territories in 1990 known to have been occupied in 1989

Multiway frequency analysis

Three, three-way frequency analyses were performed to develop saturated non-hierarchical logit models (Tabachnick and Fidell, 1989; Norušis, 1990b) of each of the binary dependent variables 'territory occupancy' , 'breeding' or 'success' (value of 'yes' or 'no') with year (value of '1989' or '1990') and area (value of 'mid-Wales' or 'mid-Argyll'). Multi-way frequency procedures are used to simultaneously test for associations between three or more discrete variables (categorical or qualitative) by comparison between observed and expected frequencies in cells produced by multi-way cross classification tables. Logit models are a special class of these procedures where there is one dichotomous dependent variable. In a saturated model all possible effects (interactions between variables) are considered. In a non-hierarchical design only statistically significant associations are retained, whereas in a hierarchical (or nested) design all lower order effects contained within the highest order interaction which is significant are retained (variable A x B is a second order interaction; A x B x C is a third, and higher, order interaction). Non-hierarchical methods are most suitable when, as here, the goal is to identify and interpret statistically significant associations. Multi-way frequency analyses are preferable to repeated Chi-square tests of independence for each sub-table as these do not permit estimates of the effects of variables on each other, as well as requiring multiple null hypotheses.

Occupancy

The analysis produced a model which included only the first order effect of the dependent variable 'occupied', and one two-way association: occupancy by area. All component two-way contingency tables showed expected frequencies in excess of five (as in Chi-square tests, the requirement is that no expected cell frequency should be less than one, and no more than 20% of cells less than five). The model had a likelihood ratio chi square $G^2_2=1.35$, $p=0.59$, indicating a good fit between observed frequencies and expected frequencies generated by the model. A summary of the model with z scores, results of tests of significance and loglinear parameter estimates appears in Table 4.3. The first order effect of occupancy and the second order effect between occupancy and area were significant at the $p<0.01$ level, with no other effects significant at $p = 0.05$. The first order effect indicated that there were more occupied than unoccupied territories in the sample. The second

order interaction indicated that occupancy of known territories was significantly greater in mid-Wales than mid-Argyll. There was no indication of a difference between years.

Effect	z score (p)	Loglinear parameter estimate (lambda)	
		No	Yes
occupied	-11.70 **	-0.995	0.995
occ. by area	-3.75 **	Wales: -0.391	0.319
		Argyll : 0.319	-0.319

Table 4.3. Summary of logit model of territory occupancy between mid-Argyll and mid-Wales, and years 1989 and 1990.
**p<0.01.

To support this finding, when only sites in 1990 which were occupied in 1989 were considered (Table 4.2) there was a significantly higher proportion of sites re-occupied in mid-Wales than mid-Argyll (*G*-test with William's correction factor: G_{adj}= 19.25, df = 1, p < 0.001).

Breeding attempts

The analysis produced a model which included only the first order effect (breeding), one second order effect (breeding by area) and the three-way association (breeding by area by year). All component two-way contingency tables showed expected frequencies in excess of five. The model had a likelihood ratio Chi Square G^2_2= 0.11, p=0.74, indicating a good fit between observed frequencies and expected frequencies generated by the model. A summary of the model with *z* scores, results of tests of significance and loglinear parameter estimates appears in Table 4.4. Only the first order effect of the dependent variable, breeding, and the second order effect between breeding and area were significant at the p<0.01 level. The first order effect indicated that at occupied sites more pairs made a breeding attempt than did not. The second order effect indicated that the proportion of occupied territories in which breeding was attempted was higher in mid-Wales than mid-Argyll. There was no significant association with year overall, but the third order effect (not significant at p < 0.01 level) indicated that there were proportionately fewer breeding attempts in mid-Wales and/or more in mid-Argyll in 1989 than 1990.

Effect	z score (p)	Loglinear parameter estimate (lambda)	
		No	Yes
Breeding	-10.11 (**)	-1.318	1.318
Brd. by area	-3.34 (**)	Wales: -0.403	0.403
		Argyll: 0.403	-0.403
Brd. by area by year (1989)	2.38 (*)	Wales: 0.276	-0.276
		Argyll:-0.276	0.276

Table 4.4. Summary of logit model of proportion of breeding attempts in the population between mid-Argyll and mid-Wales, and years 1989 and 1990.
*p<0.05, **p<0.01.

Breeding success

The analysis produced a model which included only the first order effect of the dependent variable (success) and one two-way effect (success by area). All component two-way contingency tables showed expected frequencies in excess of five. The model had a likelihood ratio chi square G^2_2=3.40 p=0.18, indicating adequate fit between observed frequencies and expected frequencies generated by the model. A summary of the model with results of *z* scores, tests of significance and loglinear parameter estimates appears in Table 4.5. Only the first order effect of the dependent variable, breeding success, was significant at the p<0.01 level: of pairs which attempted to breed more were successful than failed. The second order interaction between success and area, not significant at the p < 0.01 level, indicated that mid-Wales breeding attempts were less successful than mid-Argyll. The proportion of territories which were successful did not differ between years.

Effect	z score (p)	Loglinear parameter estimate (lambda)	
		No	Yes
Success	-5.77 (**)	-0.442	0.442
Suc. by area	2.01 (*)	Wales: 0.155	-0.155
		Argyll:-0.155	0.155

Table 4.5. Summary of logit model of proportion of successful breeding attempts in the population between mid-Argyll and mid-Wales, and years 1989 and 1990.
*p<0.05, **p<0.01.

Differences in breeding performance between years and sites

A summary of clutch size, hatched brood size and numbers fledged is presented in Tables 4.6. and 4.7. The distribution of the weeks in which each pair commenced laying in each year is shown for mid-Argyll and mid-Wales in Figure 4.2. When comparing these parameters between years and areas it would have been preferable to use a multi-way frequency approach for many analyses, to permit interaction terms between year and site to be considered. However, small sample sizes resulted in component two-way contingency tables with many cells having expected frequencies of less than one and over 20% of cells with less than five. I have therefore restricted analyses to univariate comparisons of central tendency or correlations. Except where stated, data were not normally distributed and non-parametric statistical techniques were used to investigate differences between groups, the null hypothesis being that there were no differences between groups. Two-tailed tests were used throughout.

	Median clutch	max : min	n	Median hatched	max : min	n
Argyll 1989	5.0	8 : 3	14	-	-	0
Argyll 1990	5.0	6 : 4	9	-	-	0
Wales 1989	5.5	7 : 3	24	4.0	6 : 1	7
Wales 1990	5.0	7 : 2	30	5.0	5 : 2	5

Table 4.6. Summary table of clutch size (mid-Argyll and mid-Wales) and number of young hatched in nests successfully hatching at least one young (mid-Wales only).

	No. fledged per successful pair			No. fledged per breeding pair		
	Median	max : min	n	Median	max : min	n
Argyll 1989	3.0	5 : 1	28	2.0	5 : 0	34
Argyll 1990	3.0	6 : 1	31	2.0	6 : 0	45
Wales 1989	3.0	6 : 1	43	1.0	6 : 0	73
Wales 1990	3.5	5 : 1	46	2.0	5 : 0	69

Table 4.7. Summary table of fledged brood size for successful pairs and all pairs where breeding outcome was known.

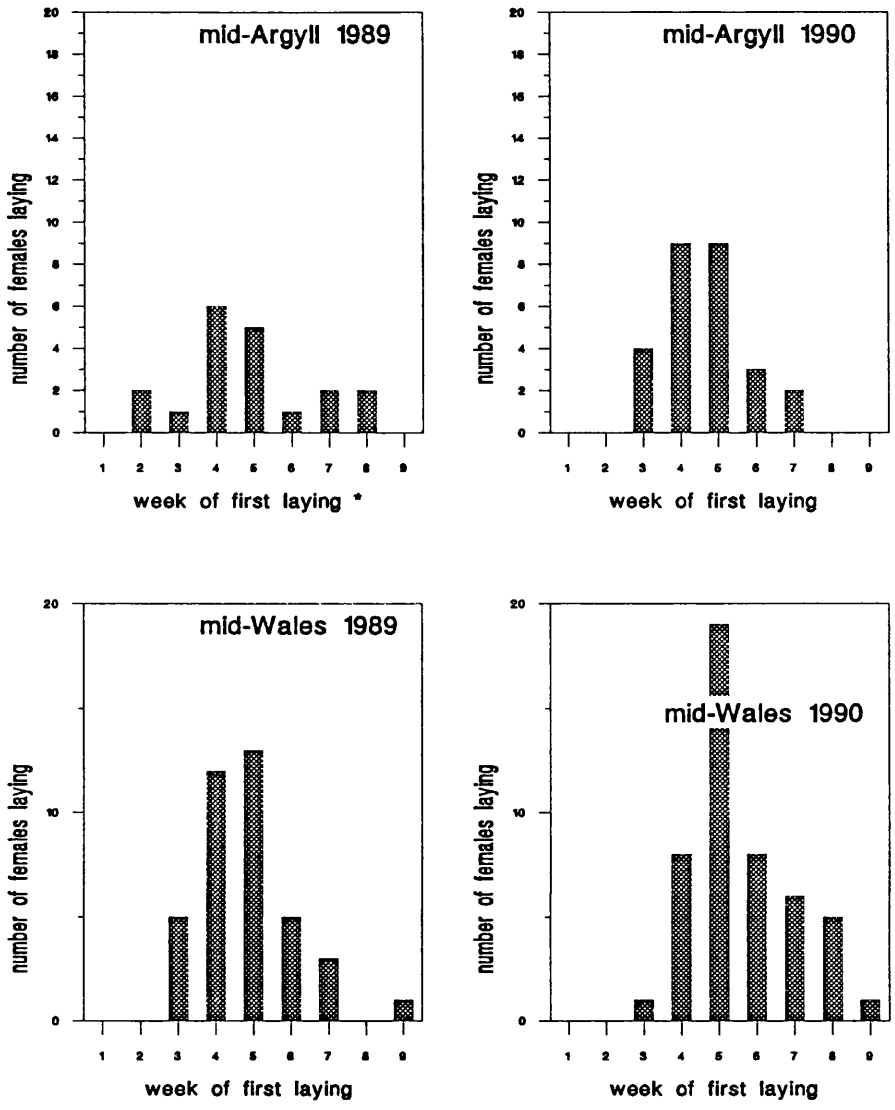

Figure 4.2. Distribution of week of first laying in mid-Argyll and mid-Wales in 1989 and 1990.
Weeks were designated as 7 day intervals beginning 1st February each year.

Clutch size

There was no significant difference in clutch size between years within mid-Argyll (Mann-Whitney U=48.0, p=0.31) or mid-Wales (M-W U=314.0, p=0.41), and there was no difference in clutch size between the two areas when data for both years were combined (M-W U=525.0, p=0.26).

Number hatched

There was no significant difference in the number of young hatched in nests successfully hatching eggs between years in mid-Wales (M-W U=14.0, p=0.54). Hatching success was not recorded in mid-Argyll due to the difficulty in reaching nests.

Number fledged

There was no significant difference in the number of young fledged in successful nests between years in mid-Argyll (M-W U=431.0, p=0.96) or mid-Wales (M-W U=842.5, p=0.21), or between the two areas when both years were combined (M-W U=2392.5, p=0.34). There were no significant differences in the number of young fledged by all pairs between years in mid-Argyll (M-W U=665.0, p=0.31) or mid-Wales (M-W U=2188.0, p=0.13), nor between areas when both years were combined (M-W U=5178.5, p=0.29).

Timing of breeding

In mid-Argyll there was no significant difference in week of first laying between years (M-W U=243.0, p=0.75), however, in mid-Wales laying week was significantly earlier in 1989 than in 1990 (M-W U=627.5, p=0.006). In 1989 there was no significant difference in laying week between the two areas (M-W U=367.5, p=0.95), but in 1990 laying commenced significantly earlier in mid-Argyll than mid-Wales (M-W U=387.5, p=0.003). When data for both years were combined laying week in mid-Argyll was significantly earlier than in mid-Wales (M-W U=1568.0, p=0.03).

Differences in breeding performance with timing of breeding

Differences in breeding success, clutch size and fledged brood size of successful pairs were examined by correlating each variable with absolute laying week, relative laying week within a site/year group, and early and late groupings. Relative laying week was calculated for each year and site by subtracting the laying week for each case from the median laying week for that site/year, and the laying season for each site/year was divided up into early (<median laying week) and late (≥ median laying week).

Clutch size

There was no significant correlation between clutch size and absolute laying week (Spearman's Rank Correlation coefficient r_s=-0.11, n=36, p>0.05) or relative laying week (r_s=0.29, n=36, p>0.05). There was no significant difference between clutch size of early or late breeders (M-W *U*=111.5, p=0.19).

Hatching and fledging success in mid-Wales

There was no significant correlation between the proportion of eggs successfully hatching (r_s=0.34, n=6, p>0.05) or fledging (r_s=0.19, n=31, p>0.05) with laying week, in mid-Wales. There were insufficient data to make a comparison of proportion of eggs fledging with laying week in mid-Argyll. There was no significant correlation between fledged brood size of successful pairs and absolute laying week (r_s=0.06, n=85, p>0.05) or relative laying week (r_s=0.11, n=85, p>0.05). There was no significant difference between fledged brood size of early or late successful breeders (M-W *U*=726.5, p=0.07).

Breeding success

There was no significant difference between successful and unsuccessful breeding attempts in absolute laying week (M-W *U*=210.0, p=0.08), relative laying week (M-W *U*=226.0, p=0.15), or between early and late breeders (M-W *U*=498.5, p=0.87).

Differences in breeding performance with nearest neighbour distance.

For each sample considered, nearest neighbour distance (NND), 1989 clutch size in mid-Wales, and 1990 clutch size and successful fledged brood size in mid-Argyll were normally distributed, and parametric tests were used to examine differences. Successful fledged brood size in 1989 in mid-Wales was not normally distributed however and a non-parametric approach was required. There was no significant correlation between clutch size of pairs laying eggs and NND in mid-Wales in 1989 (Pearson correlation coefficient r=0.40, n=16, n.s.) or mid-Argyll in 1990 (r=-0.01, n=7, n.s.). There was no significant correlation between fledged brood size of successful pairs and NND in mid-Wales in 1989 (r_s=-0.30, n=31, n.s.) or mid-Argyll in 1990 (r=-0.17, n=24, n.s.). There was no significant difference between the mean NND of successful and

unsuccessful pairs in mid-Wales in 1989 (Student's t_{56}=1.13, p=0.26) or mid-Argyll in 1990 (t_{40}=-0.98, p=0.34). NND and week of first laying were not significantly correlated in mid-Wales in 1989 (r_s=0.19, n=26, n.s.) or in mid-Argyll in 1990 (r_s=0.27, n=16, n.s.). Thus, there were no detectable relationships between breeding success, performance, or timing and NND in either population.

Were territories consistent in breeding success, performance and laying date between years?

There was a significant correlation between rank score of relative laying week between years (r_s=0.59, n=31, p<0.01). There was no significant correlation between rank score of clutch size in each year for those pairs known to have completed a clutch in both years (r_s=0.29, n=15, p>0.05), or between rank score of fledged brood size in each year for those pairs known to have successfully fledged in both years (r_s=0.24, n=35, p>0.05).

Size of the non-breeding population.

A total of 433 observer hours were recorded in foot surveys, during which 1045 km were walked. These transects covered all regions of the study area, especially hill tops and ridges, and every type of habitat. Only 19 ravens were recorded which could not be positively associated with a breeding site. These occurred in singles or small groups of up to four, and throughout the area.

Road observations were logged for approximately 10000 km of travel during 210 observer hours, during which only eight ravens, in singles or doubles, were seen which could not be positively associated with a breeding site. Again road transects covered the entire study area and range of habitats , but in this case usually in valley bottoms where the roads ran. By combining counts from both hill and road logs and making the assumption that each sighting was of a different bird, I estimate that the ratio of territory to non-territory holding individuals was approximately 5:1. These assumptions are liberal and this figure should be interpreted only as a relative guide for comparison with other studies. Due to the few observations I made no attempt to break down observations by habitat or locality.

CONCLUSIONS

Ravens occupied territories at a higher overall population density in mid-Wales than in mid-Argyll. This was because pairs were closer together in the former rather than a higher proportion of the ground being unoccupied in the latter. In each area the distribution of pairs showed a tendency towards regularity, as would be expected given their territorial nature. Overall there were fewer traditional territories remaining unoccupied in mid-Wales than in mid-Argyll. This result was not an artefact of a longer record of raven territories in mid-Wales, as there was a significantly greater re-occupation of territories in 1990. For every occupied territory there were more attempts to breed in mid-Wales than in mid-Argyll, but for those breeding attempts there was no difference in success between areas. There were no differences between areas in the number of eggs laid or young fledged. All of these findings were consistent between the two years of the study.

The date of first laying was later in 1990 than in 1989 in mid-Wales, whereas there was no difference between years in mid-Argyll. When the two years were considered together mid-Argyll appeared earlier than mid-Wales, due to the lateness of the mid-Wales season in 1990. These results are at first surprising as Hollyoak (1967) found first laying date later with increasing latitude for ravens breeding in Britain, with a mean difference of two weeks between the most southerly and northerly populations. The results in this study may have agreed with Hollyoak's if a longer span of data were available for comparison. However, most ravens in mid-Argyll were near the coast which has a mild winter climate similar to mid-Wales. Dare (1986a) reported no differences in timing between two adjoining upland regions of north-Wales, but these regions were one to two weeks later than low lying Anglesey nearby. Mid or late winter isotherms may be a more reliable predictor of first laying date than latitude. Clearly, the effects of local conditions can contribute much to the lateness of the raven laying period. Late nests were just as successful as early ones: there were no detectable relationships between breeding performance and timing of breeding. Timing of breeding was however consistent between years at individual sites, whereas clutch size and fledged brood size (successful pairs) were not. Clearly, timing of breeding was mediated by factors influencing the regional population in any one year (such as the weather) whereas breeding performance was subject to perturbations acting at a level which could vary between

territories and years. There appeared to be no relationship between the size of the territory, inferred from NND, and any measure of breeding performance or timing of breeding considered. This result was consistent between both mid-Argyll and mid-Wales, with very different overall population densities, and between years.

There appeared to be very few non-territorial birds in mid-Argyll in 1990, and no different from my subjective impressions obtained during 1989. In mid-Wales by contrast, the size of this population during the breeding season was estimated to be equal to the number of breeding birds in 1975-79 (Newton *et al.* 1982; Davis and Davis, 1986) Personal observations in this area by myself (1982-84), and A.C. Cross (1986 to present) agree with this estimate.

PART II. REGIONAL DIFFERENCES IN DENSITY, OCCUPANCY AND BREEDING PERFORMANCE IN THE BRITISH ISLES

ANALYSIS AND RESULTS

Raven population density and mean NND are presented in Table 4.8 for regions of Britain for which published information is available. Caution is needed in comparing these studies as the exact methodology used in calculations may have varied and was not always apparent in published accounts. Calculations of density depend on the size of the enclosing area: this may be some convenient boundary, such as the limits of a county, or may be defined by the fieldworker. In the first case such an area may contain much ground that is unsuitable for ravens, whilst in the second case study areas are often delineated by the boundary of suitable habitat. This will lead to lower reported densities in the first type of study area than would have been the case if only 'raven country' had been considered. In addition some workers, especially in long term studies, count territories, which may include irregularly occupied territories, rather than breeding pairs, as in this study. Studies reporting a single year's census will not include territories unoccupied that year, whereas over several years many more territories will have been occupied, at least for a limited period. Density is best considered in conjunction with NND as this is likely to be a more standard measure, and permits an insight into the 'patchiness' of raven distribution within the study area.

The relationship between observed NND and reported density was compared with the theoretical NND of randomly distributed sites and reported density to examine regional differences in dispersion. Expected NND was calculated from the formula given in Section A2.1 for each reported density where mean NND was also given. The two distributions are shown in Figure 4.2.

location	years	area (km^2)	No. pairs	Density (pairs/km^2)	NND	s.d.	n (NND)	Source
Shetland	82-84	1440	196	13.6	2.5 [a]	0.8	124	Ewins *et al.*, 1986
Orkney (mainland)	72-77	523	23	4.4	3.5 [b]	0.6	8	Booth, 1979
Central/SW Perthshire [c]	86-87	c1500	c21	c1.4	-	-	-	Stirling-Aird, 1988
South Ayrshire	45-70	-	-	-	4.7 [d]	1.3	24	Marquiss *et al.*, 1978
Galloway	45-70	-	-	-	2.8 [d]	1.3	28	"
Galloway Hills	49-61	435	23	5.2	2.7	-	-	Ratcliffe, 1962
Monaive	45-70	-	-	-	3.5 [d]	0.9	14	Marquiss *et al.*, 1978
Leadhills	45-70	-	-	-	5.2 [d]	0.7	13	"
Moffat and Tweedsmuir	45-70	-	-	-	4.0 [d]	1.5	18	"
Moffat Hills	49-61	497	11	2.2	4.7	-	-	Ratcliffe, 1962
Northumberland	45-70	-	-	-	6.8 [d]	2.6	20	Marquiss *et al.*, 1978
Lake District	49-61	1129	67	5.9	2.7	-	-	Ratcliffe, 1962
Isle of Mann	86	588	c40	6.8	-	-	-	Cullen and Jennings, 1986
Snowdonia	49-61	663	38	5.6	2.7	1.1	-	Ratcliffe, 1962
Snowdonia	75-85	926	97	10.5	2.0	0.6	96	Dare, 1986a
Migneint-Hiraethog	78-85	477	20	4.2	3.6	1.0	19	"
mid-Wales	75-79	475	79	17	1.8	-	-	Newton *et al.*, 1982
mid-Wales [e]	1989	587	65	11.1	1.9	0.7	66	this study
mid-Argyll (total) [e]	1990	1689	62	3.6	3.6	1.2	59	"
mid-Argyll sub-areas:								
Cowal [e]	1990	129	7	5.4	2.8	0.9	7	"
Glens [e]	1990	283	5	1.8	4.2	1.2	4	"
Lorn [e]	1990	635	26	4.1	3.2	0.8	26	"
Mull [e]	1990	552	17	3.1	4.1	1.5	17	"
Tiree [e]	1990	90	7	7.8	3.5	0.8	5	"

Table 4.8. Raven population density and mean nearest neighbour distance for areas of Britain.

a : excludes 12 sites where mean NND = 1.8.
b: highest linear mean NND.
c:: incomplete survey
d: calculated from Figure 1 in Marquiss *et al.*, 1978
e: occupied sites only

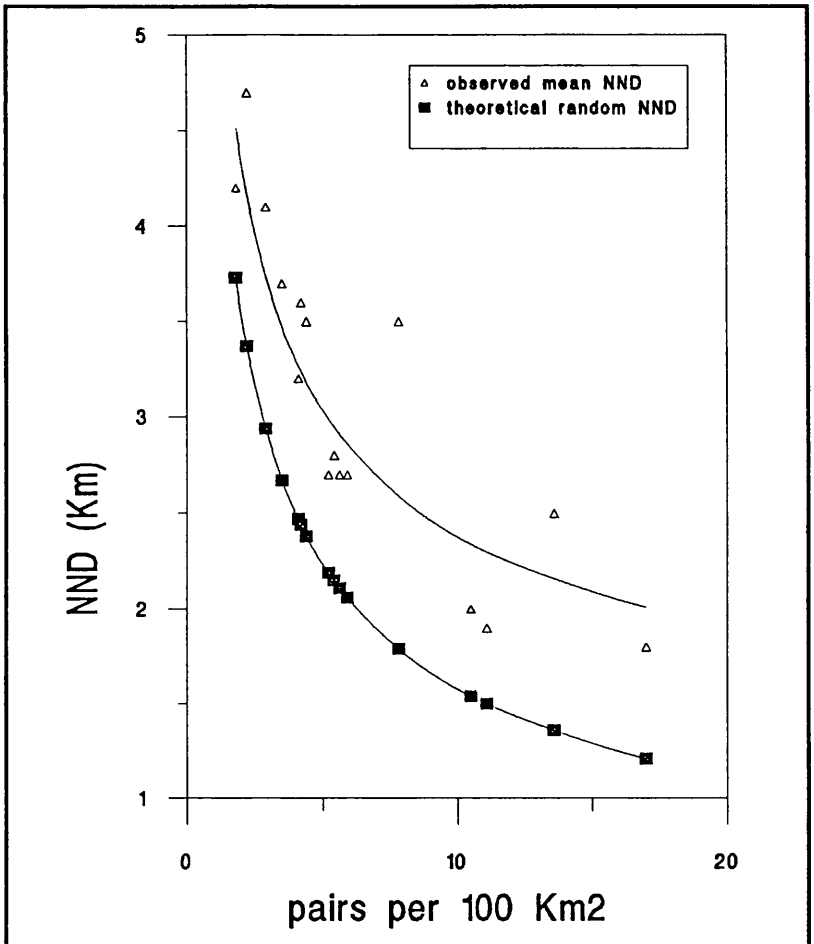

Figure 4.2. Observed and theoretical random distribution of nearest neighbour distance (NND) versus population density.
Identical curves based on interpolation of theoretical distribution fitted by eye.

These were transformed to linearity using the equation

$$y = \left\langle \frac{1}{2(NND)} \right\rangle^2$$

and plotted against reported density (Figure 4.3). There was a significant linear relationship between both observed NND ($y_{observed} = 0.0061 + 0.0041x$; $r^2 = 0.764$; $p < 0.001$)and theoretical random NND ($y_{random} = 0.01x$; $r^2 = 1.000$; $p < 0.001$) with density (pairs/100km^2).

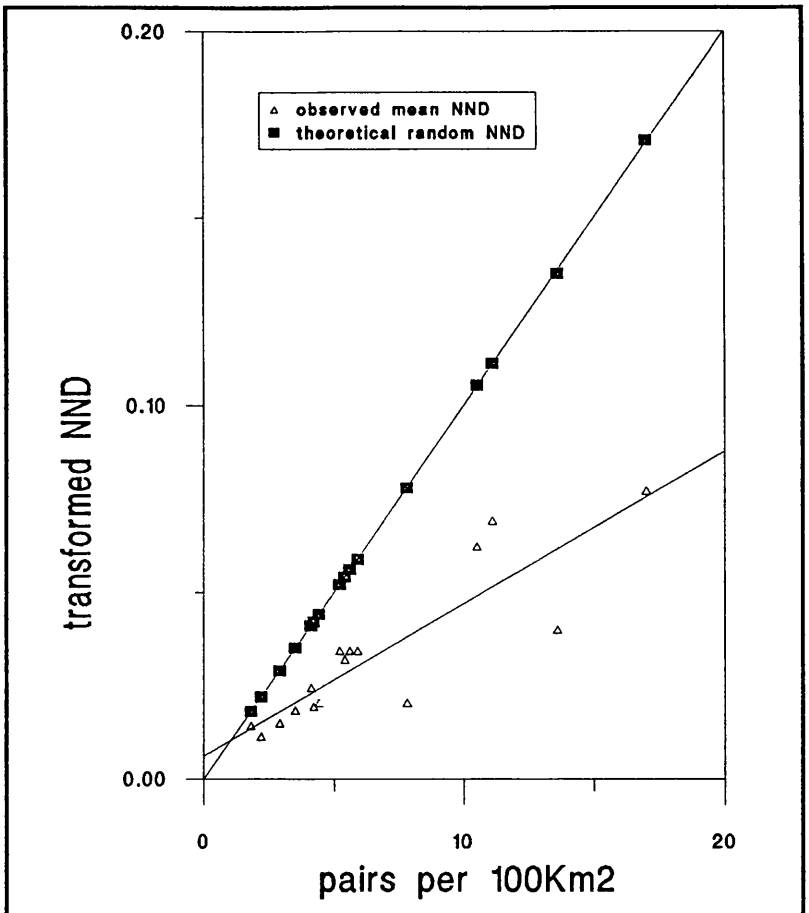

Figure 4.3. Transformed observed and theoretical random distribution of nearest neighbour distance (NND) versus population density.

Transformation: $y = \left\langle \frac{1}{2(NND)} \right\rangle^2$

regression lines: $y_{observed} = 0.0061 + 0.0041x$ ($r^2 = 0.764$; $p < 0.001$)

$y_{random} = 0.01x$ ($r^2 = 1.000$; $p < 0.001$)

An analysis of covariance was performed using the SPSS procedure MANOVA. There was no significant difference in the slopes of the two regression lines ($F_{1,28} = 0.25$; $p = 0.588$; n.s.) but there was a significant difference in regression line elevations ($F_{1,29} = 32.25$; $p < 0.001$). The regression of observed NND against density was based on mean data, as complete data were not available from published studies, and therefore variation around points was not included in the analysis. However, it seems clear that in every area considered

the nearest neighbour statistic R was greater than one, indicating a tendency towards a regular dispersion, and that this value did not vary significantly over a range of densities.

The proportion of breeding attempts which were successful in producing at least one fledged young were available for seven areas in addition to mid-Wales and mid-Argyll (Table 4.9). The distribution of observed proportions were significantly different from the expected proportions ($\chi^2_8 = 22.45$, $p < 0.01$) indicating an overall difference in breeding success between sites. I examined Bonferroni probability statements for the 95% family of simultaneous confidence intervals to determine where differences between the observed and expected proportions lay (Neu et al., 1974). Confidence limits are constructed for the true proportion successful in the population, P, from the observed proportion successful, p_i, in each study using the Bonferroni inequality given below:

$$p_i - Z_{\alpha/2k}\sqrt{\langle pi(1-pi)/n\rangle} \leq P \leq p_i + Z_{\alpha/2k}\sqrt{\langle pi(1-pi)/n\rangle}$$

where

k is the number of studies (= 9)

α is the significance level (= 0.05)

$Z_{\alpha/2k}$ is the upper standard normal table value corresponding to a probability tail area of $\alpha/2k$ (= 2.77)

Calculated confidence intervals are shown in Table 4.9. If the ranges of confidence intervals did not overlap between two studies then there was no significant difference between them. There was a significant difference only between mid-Argyll and Shetland. Causes of nest failure from several studies are given in Table 4.10.

location	n	proportion successful (p_i)	simultaneous 95% confidence interval *	$\leq P$	$P \leq$	source
Snowdonia	86	0.733	± 0.132	0.601	0.865	Dare, 1986a
Migneint-Hiraethog	22	0.727	± 0.263	0.464	0.990	"
Orkney	81	0.568	± 0.152	0.416	0.720	Booth, 1985
Shetland	133	0.519	± 0.120	0.399	0.639	Ewins *et al.*, 1986
mid-Wales	245	0.665	± 0.084	0.581	0.749	Newton *et al.*, 1982
south Scotland	23	0.739	± 0.254	0.485	0.993	Mearns, 1983
Isle of Man	25	0.720	± 0.249	0.471	0.969	Cowin, 1941
mid-Wales	149	0.644	± 0.109	0.535	0.753	this study
mid-Argyll	86	0.825	± 0.113	0.712	0.938	"

Table 4.9. Proportion of breeding attempts successfully producing ≥ 1 fledged young from different areas of Britain.
* Bonferroni probability statements, see text

location	human (%)	fulmars (%)	other (%) *	unknown (%)	source
Shetland	21 (33)	14 (22)	2 (3)	27 (42)	Ewins *et al.*, 1986
Orkney	12 (27)	6 (13)	1 (2)	16 (36)	Booth, 1985
Snowdonia	7 (30)	0 (0)	3 (13)	13 (57)	Dare, 1986a
Mid-Wales	44 (44)	0 (0)	5 (5)	50 (50)	Davis and Davis, 1986
Mid-Argyll	1 (5)	0 (0)	0 (0)	19 (95)	this study
s.Scotland n.England	negligible	none			Marquiss *et al.*, 1978

Table 4.10. Causes of nest failures in regions of Britain.
* includes: disturbance from competitors (peregrine falcon, golden eagle); infertile eggs; nest collapse.

Clutch sizes and fledged brood sizes of successful pairs reported in a form suitable for statistical comparison are presented in Tables 4.11 and 4.12. A Kruskal-Wallis one-way analysis of variance by ranks (corrected for ties) showed that there was a significant difference in clutch size between groups ($KW_5 = 22.5$, $p < 0.001$) and in fledged brood size between groups ($KW_6 = 18.4$, $p < 0.01$). A multiple comparison procedure was used to determine which groups were different (Siegel and Castellan, 1988, page 213). For differences in clutch size the null hypothesis of no difference between groups could be rejected at the threshold of $p = 0.05$ for only two

comparisons: median clutch size of a sample measured on the Isle of Man was significantly lower than in mid-Wales in 1975-79 and 1989-90. The null hypothesis could be rejected only for one comparison of fledged brood size between groups: the median value for the sample from Ratcliffe's (1962) four regions was significantly lower than for mid-Wales in 1989.

location	clutch size								median	source
	1	2	3	4	5	6	7	8		
Isle of Man	5	8	15	9	24	5	4	0	4.0	Cullen and Jennings, 1986
5 regions	0	3	10	43	60	23	0	0	5.0	Ratcliffe, 1962
mid-Wales	2	5	19	33	37	27	1	0	5.0	Davis and Davis, 1986
Orkney	0	0	0	3	7	5	0	0	5.0	Booth, 1979
mid-Argyll	0	0	2	6	11	3	0	1	5.0	this study
mid-Wales	0	2	3	11	18	16	4	0	5.0	"

Table 4.11. Clutch sizes from different areas of Britain

location	fledged brood size						median	source
	1	2	3	4	5	6		
Isle of Man	11	31	37	23	4	1	3.0	Cullen and Jennings, 1986
4 regions	23	42	23	29	2	1	2.0	Ratcliffe, 1962
mid-Wales	25	41	50	36	13	0	3.0	Davis and Davis, 1986
Snowdonia	3	16	9	3	1	0	2.0	Dare, 1986a
Orkney	6	11	13	16	6	0	3.0	Booth, 1979
mid-Argyll	5	17	18	14	4	1	3.0	this study
mid-Wales	12	10	31	29	5	1	3.0	"

Table 4.12. Fledged brood sizes from different areas of Britain.

Published estimates of the size of the non-territorial flock, during the breeding season, were available from three regions in Britain in addition to mid-Argyll. The ratio of non-territorial birds to territorial birds (pairs x 2) was plotted against population density (Figure 4.4). Dare's (1986a) values for Snowdonia and Migneint-Hiraethog were combined (as 'north-Wales') as the two study areas were contiguous and non-territorial birds may have wandered over the distances involved. These figures are only estimates of the true ratio, given the difficulty of measuring this in the field, and serve only to point out possible trends.

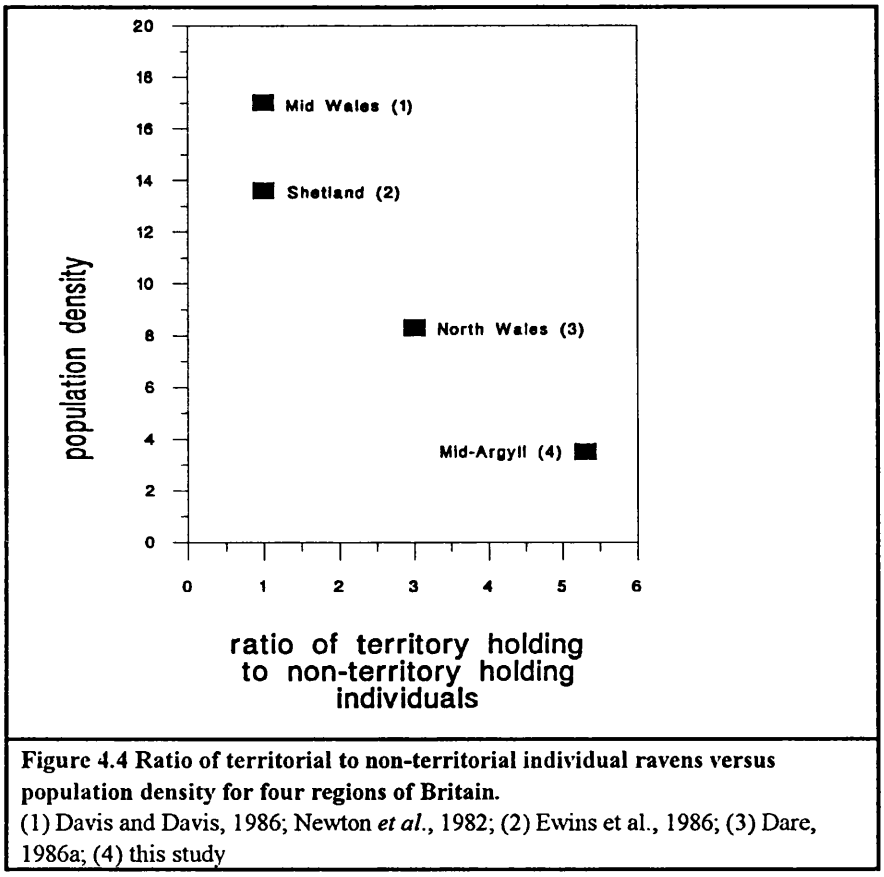

Figure 4.4 Ratio of territorial to non-territorial individual ravens versus population density for four regions of Britain.
(1) Davis and Davis, 1986; Newton *et al.*, 1982; (2) Ewins et al., 1986; (3) Dare, 1986a; (4) this study

CONCLUSIONS

Territorial ravens in all areas tend to be regularly dispersed, with no significant differences in this tendency over a 10 fold difference in population density. Thus it appears that for areas populated by ravens, those holding lower densities do so because of an increase in spacing between pairs rather than the existence of a higher proportion of unsuitable ground (which would lead to a clumped distribution within the study area), when considered on a regional scale. However, the nearest neighbour statistic calculated at this scale is relatively insensitive to local irregularities in spacing caused by unsuitable habitat. There was only one detectable difference in the proportion of nests which were successful across their range in Britain: ravens in Shetland were significantly less successful than in mid-Argyll. This was probably due to the latter area not only suffering very little human disturbance compared to many other areas, but also the additional source of

failure due to fulmars (*Fulmarus glacialis)* on Shetland (Table 4.10) rather than differences in habitat quality. There were few detectable differences in clutch or fledged brood size in different regions, and these were slight. Such differences are more likely ascribed to variations in observer methods, or the number of years over which studies spanned, rather than to habitat quality. Certainly, high density raven populations were no more productive than those breeding at low population density. There was no evidence to support Hollyoak's (1967) apparent decline in clutch size of ravens with increasing latitude, or, within Britain, Lack's (1947) conclusion that raven clutch size decreases from south to north across Europe.

Comparable data were few but there appeared to be a positive relationship between the number of non-territorial individuals present during the breeding season and population density, with proportionately more present at higher densities (Figure 4.4). Marquiss *et al.,* (1978) observed no non-territorial birds in their 4 large study areas (densities not available but from reported NND I estimate from Figure 4.2 that these were all low, from 2-4 prs/100 km^2) and there were apparently few in mid-Argyll, indicating that in some low density populations there may be very few non-territorial birds present in the breeding season. As this group includes sexually immature individuals, the number of potential recruits to the breeding population in any one year is likely to be even smaller.

DISCUSSION

Both detailed studies in mid-Argyll and mid-Wales, and comparison of studies throughout Britain, show that ravens breed at a great range of densities, and that this is accounted for by a greater spacing between nests (and ,by inference, an increased territory size). Though based on circumstantial evidence it is repeatedly inferred that spacing of raven territories is related to food supply. Several authors have noted the contrast between the high raven density found in mid-Wales, which is productive for a hill area with only slightly acid mineral soils (Davis and Davis, 1986), and the barren, very acid and unproductive deer forests of the western Highlands (Ratcliffe, 1962; Hollyoak and Ratcliffe, 1968; Newton *et al.* 1982). Marquiss *et al.*, 1978, related density to one source of food, namely carrion, which occurred in greater numbers on higher ground. Newton *et*

al., (1982), also found more carrion on higher ground but did not find a greater density of ravens there than in areas of lower elevation. However, pastoral land-use at lower elevations in mid-Wales may have provided more food in addition to carrion, not available on lower ground in Marquiss's region (Newton *et al.*, 1982). High raven densities in Shetland are probably related to the high availability of sheep carrion in combination with a wide range of abundant food sources from the coast. In Orkney, where coastal items are also abundant but sheep carrion is relatively scarce, ravens occurred at much lower density (Ewins *et al.*, 1986). More convincing evidence that spacing is related to food supplies comes from the studies by Ratcliffe and Dare in Snowdonia (reported in Dare, 1986a). In this region the raven population increased by 80% in a 25 year period up to the late 1970's. This was coincident with an increase in sheep numbers, and by assumption carrion supply. In the 1950's the population was as regularly distributed as in later years, but NND was significantly greater in the former period than the latter. Thus a redistribution of pairs occurred based on closer spacing.

Regional differences in raven density are difficult to explain in terms of competitors for carrion. Golden eagles are absent from mid-Wales, but here red kites and buzzards are at high density (Newton, 1982; Davis and Newton, 1981). Most sheep carrion on the open hill is eaten by foxes (Hewson, 1981), but ravens do not occur at higher densities where these are absent, for example on many Hebridean islands, compared to adjacent mainland where foxes are present. Eagles may displace ravens from nest-cliffs (Marquiss *et al.*, 1978), but there are no indications that inter-specific competition sets an upper limit on raven numbers, although local distribution may be affected. This is considered in greater detail in chapter nine.

An investigation of differences in breeding performance between mid-Wales and mid-Argyll ideally requires many years' data. The two years' data presented here offer no more than a 'snapshot' in which annual perturbations may have obscured real differences. However, conclusions drawn from this comparison were in agreement with those comparing studies from many different areas of Britain. On a regional scale breeding success was not related to population density, nor on a local scale to NND in mid-Wales or mid-Argyll, and thus appears to be density independent in British ravens. Spacing appears to be maintained at a level which ensures adequate food supplies for the production of young and maintenance of adults, as has been previously

noted by Ratcliffe (1962). However, this does not imply that all territories will do equally well in any one year, as small scale perturbations in food availability and habitat quality, in addition to chance events affecting survival of nests and young, will still have a large effect; but such effects are density independent.

Changes in habitat within the territory have been demonstrated to affect breeding production. Marquiss *et al.* (1978), found that increased amounts of afforestation in territories led to a greater tendency for non-breeding, smaller clutch sizes and smaller fledged broods. This may seem at first to be at odds with the general conclusions drawn above. However, in these cases the reduction in breeding performance was due to rapid change of the habitat quality of portions of territories that were planted with conifers. These changes brought about significant changes in diet as food availability changed. In many cases continuing decline in territory quality (as the forests matured) resulted in eventual desertion. It seems likely that these habitat changes will, in the long-term, force a new distribution of raven territories with fewer pairs occupying larger areas to produce a stable population. Observations to support this have been reported: as gaps in a distribution appear, adjacent pairs extend their range (Marquiss *et al.*, 1978; Davis and Davis, 1986).

The speed at which a new stable distribution could occur in response to habitat change will vary between regions, dependent on factors such as the availability of nest sites, turnover of breeding individuals, number of potential recruits and the continuing pace of habitat change. It should be noted that the increase in food supply in Snowdonia probably applied in even measure to all areas; that potential nest sites were abundant; and there was a non-territorial population present in the area. In this case a relatively rapid new distribution of pairs may be more likely than a situation such as that caused by afforestation, which affects only some individual territories, whilst others remain unaffected (and thereby resistant to change) or where potential new nest sites or recruits are in short supply. Newton *et al.*, (1982) , in contrast to Marquiss *et al.*, (1978), could detect no detrimental effect of afforestation on ravens breeding in central-Wales. Their conclusion that the blanket afforestation of northern England and southern Scotland was responsible for more desertions than the more fragmented pattern of planting in mid-Wales area seems entirely reasonable. However, as I discussed in Chapter 1, there was no convincing reason for the apparent lack of observed effects on breeding ravens by

habitat loss due to afforestation. One possible solution to these seemingly contradictory findings, is that the distribution of many breeding pairs in mid-Wales had already shifted to take account of the new distribution of habitats. Conditions in mid-Wales, where there is a large non-territorial population and abundance of potential nest sites in most areas, may have permitted a more rapid response to a changed environment than in the Pennine hills.

There is also evidence of a movement of young between regions. Dare (1986b) found evidence of interchange between different regions of Wales with offspring scattering widely and a small number of long distance movements of young from north Wales to England, Ireland and south-east Scotland. Davis and Davis (1986) concluded that in central Wales juveniles probably dispersed at random and that few return to their natal hill areas. Hollyoak (1971) analysed 147 British recoveries of ringed birds and found that over half had moved over 30km from their place of birth by the first winter. Ewins *et al.* (1986) found no records of emigration of ringed birds from Shetland, but there was apparent immigration from further south in spring, with flocks of up to 50 birds in some years moving north via Fair Isle. The movements of young and mixing of populations hitherto regarded as distinct, and the turnover of breeding individuals in these populations, warrants further investigation, as there is the possibility of some areas acting as a source of recruits and others as sinks .

Information on the turnover of breeding individuals and movements and recruitment of floaters into the breeding population will be difficult to measure for any population. The low numbers of potential recruits observed in low density populations raises the possibility that ravens may not occupy these areas at carrying capacity; numbers of individuals were suspected to have exceeded the maximum number of breeding territories in the high density areas of mid-Wales and Shetland (Newton et al., 1982; Ewins et al., 1986). In the present study there was a greater re-occupancy of territories in mid-Wales than in mid-Argyll from 1989 to 1990. This indicates that there is either a higher turnover of territory holding adults (due to death, rejoining the non-breeding population, or movement between territories) in mid-Argyll, or fewer recruits, or both. In the following chapters I examined the distribution and breeding performance of ravens in the low density

population of mid-Argyll in relation to the environment, to determine if the territory holding population was at carrying capacity, or if there was poor recruitment of breeders.

The observed differences in spacing between localities has implications for studies relating habitat to territory performance. Comparison of habitat within a fixed area between sites, for example a 3km radius around the nest, may not be valid at different spacing, as these figures will represent different proportions of the home range. Ideally one should compare habitat within home range boundaries, and calibrated by utilisation of areas within this. Such data would be extremely difficult to obtain for ravens, however, in the absence of such information, habitat should be measured across a range of areas around the nest, or presumed centre of territory, both within and exceeding the NND, as home ranges may overlap. Direct comparisons will only be valid between individuals or populations at the same spacing, unless multiple comparisons are made with coverage of habitat types transformed to proportions at a range of areas.

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CHAPTER 5. DEVELOPMENT OF GEOGRAPHICAL INFORMATION SYSTEMS

INTRODUCTION

In Chapter 1, I outlined the potential of Geographical Information Systems (GIS) for dealing with spatial data in ecological research and conservation management. In the remaining chapters I will report the results of my investigation into the distribution and breeding performance of ravens in mid-Argyll in relation to environmental variables and will attempt to produce robust predictive models. Previous studies of this kind have relied upon the extraction of environmental variables by hand from paper maps. This labour intensive and time-consuming process restricted workers to considering only a few environmental variables, and within a few predetermined areas around the point of interest (in bird studies, usually the nest-site). However, one would expect a complex set of inter-relationships to exist between a generalist animal such as the raven, at or near the top of its food chain, and its environment, and also between features within that environment. In addition, the paucity of information on raven home range size and habitat utilisation make predetermined choices about the size of area to be considered at best a matter of informed guesswork. Choice of scale is another important consideration, but often practical problems limit the detail from which spatial data may be extracted. Thompson and Brown (1992) have pointed out the importance of choosing the correct scale when investigating breeding distribution and habitat utilisation in relation to vegetation diversity for a range of montane birds.

Use of a GIS provides a practical solution to these problems. By automating the process of data extraction, the user can collect great quantities of numerical data: at high spatial resolution; for a large area coverage; and for a large number of variables. In addition, GIS greatly simplifies the problem of the presentation of the results of any predictive models with their spatial component (that is, not just 'what' an effect will be but also 'where'). Furthermore, the results of separate analyses may be overlaid on these results. This may lead not only to a greater understanding of the results themselves, but can provide conservation managers with a more suitable and useful set of results from such ecological research than results presented solely as 'word' or 'statistical' models.

OBJECTIVES

Two, separate GIS systems were used for data extraction (*environment GIS*, using a system called Laser Scan Horizon) and mapping the results of statistical modelling (*analysis GIS*, using a system called PC Arc/Info). The environment GIS was used to assemble relevant environmental information (including satellite remote sensed image data) in compatible formats within the system and to construct programs to extract large and detailed data sets for statistical analyses (inductive modelling) outside the GIS. These inductive analyses were designed primarily to produce predictive models of the spatial distribution of parameters of raven distribution and breeding across the study area, rather than deduce the most important features of the environment with regard to these parameters. The analysis GIS was used to map and overlay the results of separate analyses (deductive modelling) to give an overall view of how habitat suitable for occupancy, breeding, and the availability of nest sites combined to produce the observed distribution of ravens. For example, were some observed gaps in the distribution due to a lack of nest-sites, or was the habitat unsuitable? In this chapter I will describe the design and use of both of these systems.

In broader terms, this chapter sets out to assess the usefulness of the GIS/remote sensing approach for this kind of research. Initially I had little computing experience. I therefore consider whether it is possible for a non-specialist to use these systems as tools for ecological research and obtain results more efficiently, or indeed obtain results which are simply not possible, using more traditional methods. Also, whether remotely sensed images can be used to distinguish between upland vegetation types (which often merge one into another, forming gradients rather than boundaries), in very rugged terrain, in sufficient detail to be useful for modelling. Finally, whether it was feasible to integrate complex multivariate modelling with a GIS at this stage of the technology's development. I also consider how GIS could be improved for ecological research?

CHAPTER FORMAT

An introduction to GIS, digital data and remote sensing is given first, along with a review of several wildlife studies which have made use of this technology. Part I then describes the equipment, software and methods

used to capture the initial data in digital format, to process Landsat imagery and to derive secondary data, such as a digital terrain model, and explains how these were integrated into the environment GIS. In Part II, I describe the systematic extraction of data, which used custom programs to perform these functions. In Part III, I describe how the analysis GIS was set up to display and overlay the results of statistical analysis.

BACKGROUND

What is a Geographical Information System ?

A Geographical Information System (GIS), as defined by the US National Science Foundation (in Walker and Miller, 1991), is a computerised database management system used for the capture, storage, retrieval, analysis and display of spatial (i.e., defined by location) data. A GIS has a topological data structure that is automatically generated and maintained by the system. The structure includes topological relations among the various cartographic features. Integrated within its data model, the GIS also has capabilities for managing the attribute data that are related to the cartographic data: for any cartographic feature maintained on a map, a direct link can be made to any associated descriptive or tabular information about that feature (Walker and Miller, 1991). The technology can be used to overlay and combine data into a single computerised map to summarise geographic, cultural, and scientific coverage attributes. It differs from computerised mapping software through its capacity to conduct spatial searches and overlays that actually generate new information. GIS is a new and rapidly expanding field with a great range of new applications being developed (see Walker and Millar, 1991, for an extensive review). Its potential as a planning tool for conservation managers (Haines-Young et al., 1990) and as a research tool in ecological studies (Haslett, 1990) is now well recognised.

The potential of GIS for any discipline falls into two categories: the first is as a research tool for exploring spatial relationships, and, with appropriate database structure, temporal relationships (Langran, 1989); the second is as an applied tool for data storage, management and planning; this can incorporate procedures and models developed by the research.

Until recently, GIS has been commercially developed as an applied tool, with the more specialised and demanding requirements of researchers largely ignored. In addition, a rigorous theoretical and applied framework for working with these new, spatially-rich data has needed time to evolve. This situation is rapidly changing. Scholten and Lepper (1990), reviewing the potential of the application of GIS for the World Health Organisation concluded "...[GIS] provides health researchers with new and reliable and scientifically valid methods for handling their spatial information... GIS offers the perfect working environment to describe, to investigate, to monitor or to forecast". These comments apply equally well to ecologists. An increased flexibility and power in GIS software, and the ability to add on external customised programs written in high level languages, is further improving the potential of this area for research. Openshaw *et al.* (1988, 1990), for example, have combined GIS methods with a powerful, external statistical algorithm to examine cancer clusters in relation to environmental variables in Northern England.

Digital map formats

Maps in a GIS can take one of three formats, 'vector', 'raster', and 'quadtree'. 'Vector' (also known as 'Arc-Node') format portrays features as: 1) points (nodes), e.g. for a spot height; 2) lines (arcs), e.g. for a road; or 3) polygons made up of closed lines, e.g. for a field boundary. Each of these are stored as Cartesian coordinates and each vector has a unique feature code. Attached to this is information pertaining to that feature: its map symbol, location, adjoining features, direction (by which a boundary enclosing a polygon can determine which is 'inside' and 'outside') and any subsidiary data that the operator designs into the system. Vector maps give a very precise representation of reality and are readily interpreted, being visually similar to standard linework on hard copy maps, and permit precise measurement of attributes such as location, feature length, distance from other features, and enclosed or excluded area.

In 'raster' format, locational data is stored by a regular grid of cells laid over an area. Attribute data are collected for each grid cell, known as 'individual picture elements' or 'pixels'. The size of these pixels are given in terms of the length of the side of the cell on the ground. For example, a 500m pixel resolution map stores information for each cell relating to a corresponding 500m x 500m square on the ground. These data can be

displayed as a computer screen image or hard copy, with the value of a pixel determining its representation. Only limited use can be made of attribute data stored in this way. However it is collected, stored and manipulated in a very efficient way (a simple array). A well known raster format employs quadtrees in which data are stored in grid cells of variable size. Within larger homogeneous areas a large cell size is used, elsewhere the cell size diminishes down to individual pixels. A quadtree structure permits analysis to be carried out at high speed, stores data efficiently and yet still retains a good deal of the original precision of the data, though no raster format can compete with vector format in terms of precision. The ability to integrate spatial data in different formats is a relatively recent advance in GIS technology. In this study, the system which I used for the environment GIS could process both raster and vector data sets, and convert between the two. The system used for the analysis GIS could use vector data only.

Satellite remote sensing

Remote sensing is the science of deriving information about the Earth's land and water areas from images acquired at a distance. It usually relies upon measurement of the electromagnetic energy reflected or emitted from the features of interest (Campbell, 1987). Differences in the reflected or emitted radiation from objects or areas measured from above serve as a basis for the transformation of these raw data into images representing the distribution of these features on the ground. Multispectral scanners record information within a predetermined number of wavebands, often outside the visible spectrum. Scanners may be mounted on a variety of platforms such as aircraft or orbiting or geostationary satellites in space. They record reflected or emitted radiation at a resolution determined by the sensor and height above the Earth's surface. Digital data from each waveband is stored in raster format. These data are analysed using image processing software, usually on dedicated hardware.

In this study, I used data acquired by the Thematic Mapper (TM) on board the Landsat 5 satellite launched in 1984. This device records reflected radiation in six non-overlapping wavebands with a 30m pixel IFOV (In Field of View) and emitted radiation in a seventh (thermal infra-red) band at a 120m pixel IFOV. The apparatus was specifically designed to monitor ground cover. Landsat 5 orbits at a height of 705km, and

obtains a complete coverage of the earth every 16 days, recording radiation from the Earth over a swath width of 185km. Within the image processor, different wavebands may each be assigned a different colour and overlaid. With knowledge of the properties of colour mixing, it is possible to produce a 'false colour image', from which many features present on the ground may readily be interpreted. However, these data values represent the radiation measured and not the features of interest themselves. The methods employed to classify an image and derive this information fall into one of two categories: supervised and unsupervised classification. In a *supervised classification*, features on the ground are mapped and their boundaries overlaid on the unprocessed image. The values of pixels in these areas serve as a basis for classifying all the other pixels in the image exhibiting these properties. In an *unsupervised classification*, a statistical clustering algorithm is employed to group pixels into a predetermined number of classes, and test areas are than compared with reality. Often a combination of the two are used to derive a satisfactory classification.

Deriving a classified image of ground cover can be a difficult task, especially in mountainous country (Jones and Wyatt, 1988). The amount of reflected radiation reaching the satellite will be affected by atmospheric conditions and the angle and intensity of sunlight striking the incident surface. The latter will vary with terrain; for example the reflectance from identical ground cover will be different on a sunny slope to that obtained from an adjacent one which is in shade. In addition, one may wish to differentiate between different types of ground cover which may have similar reflectance 'signatures' in the image in question. In this case, additional information must be used in the classification procedure, either from another image acquired at a different time of year when signatures may be different, or the use of ancillary data such as maps of soil or altitude. Despite these problems, satellite remote sensing of land cover has many advantages over alternatives such as ground surveys or photogrammetry. It provides a relatively cheap method of covering large areas, in some detail and to a uniform standard as precision is not compromised by increasing area of coverage, with the possibility of deriving many different classifications for different purposes, and in digital format. Its potential for ecologists is further increased by the ease with which it may be integrated into a GIS and overlaid with other spatial data, and, in the future, by development of automated data processing to allow continuous large scale monitoring (Trotter, 1991).

Previous wildlife studies which have made use of GIS and remote sensing

The use of GIS and remote sensing in wildlife studies is a rapidly growing but still fledgling research field. Most of the studies reported to date have had as their major objective the derivation of habitat suitability maps, often with a view to resource management.

Lyon (1983) used a classified Landsat MSS image as a single data set to determine the areas of potential nesting habitat of American kestrels (*Falco sparverius*) in Oregon. A model was derived using the spatial characteristics of land-cover types, found from field studies to be important to nesting birds, and tested by locating additional nesting areas separate from those used in the initial modelling. Seven out of ten predicted locations were actual nesting areas. Avery and Haines-Young (1990) were able to predict fairly accurately the numbers of dunlin *(Calidris alpina)* breeding on the flows of north-east Scotland from reflected radiation in Landsat MSS band seven, which is sensitive to variation in vegetation and ground wetness. The census of dunlin was performed in 1986, after afforestation had destroyed much of the breeding habitat, but the image used was from 1978, before the change took place. This allowed them to estimate the loss of breeding dunlin due to afforestation and demonstrated the value of archival remotely sensed data.

A combination of bird census data and a habitat classification from Landsat TM data was processed to obtain habitat suitability estimates for a range of woodland birds in Kansas by Palmeirim (1988). He considered not only the type of habitat present but also spatial characteristics such as patch size and distance to edge, and was able to automatically generate distribution, suitability and density maps of the area for each species and make rough estimates of population size. The ease with which complex measurements of habitat may be obtained within a GIS was highlighted by Shaw and Atkinson (1989) in their study of two species of warbler breeding in Texas. For the golden-cheeked warbler (*Dendroica chrysoparia*), they used Landsat MSS imagery to map a specific plant community (known from previous studies to be the only nesting habitat) across the species entire breeding range (73,000 km^2). Spatial characteristics were measured for thousands of patches of habitat (including the size distribution of patches; relation of patch size to distance from neighbouring patches; and

the convolution of patch edges) and were found to be distinctly different between regions. For the second species, the black-capped vireo (*Vireo atricapullus*), they investigated the relationship between habitat classification, topography, geology and human activities at known territory locations to identify additional areas conforming to these criteria across a 113km^2 study area.

Habitat suitability modelling is not just restricted to establishing suitability for occurrence or breeding. Hodgson *et al.* (1987; 1988) used a GIS to integrate spatial data, including Landsat TM imagery, to model quantitative foraging habitat statistics around a wood stork (*Mycteria americana*) colony in Georgia, USA. They were able to compare differences in these parameters between dry and wet years and aid the interpretation of breeding success between years of variable rainfall. Ormsby and Lunetta (1987) developed maps from Landsat TM data showing whitetail deer (*Odocoileus virginia*) food availability. The GIS model incorporated food values assigned to various land covers and 'escape' cover providing refuge from predators. Carey *et al.* (1992) incorporated radio telemetry observations of home range area and habitat use by northern spotted owls (*Strix occidentalis caurina*) into a GIS. The GIS was used to derive complex measurements of the amount and fragmentation of forest habitat (digitised from aerial photographs) in relation to these data.

The study most similar to my own was that undertaken by Pereira and Itami (1991) on Mount Graham Red Squirrels in Arizona. As in the present study, they used a GIS to manage a complex set of spatial data (but in their case only in raster format) to provide information from known areas for multivariate modelling outside the GIS. The results of this modelling were then put back into the GIS to produce predictive maps for all areas. Statistical analysis within a GIS is, at present, still in developmental stage, and was not possible in the present study. Integration of GIS with statistical routines will be a major step forward in the development of this field. Walker and Moore (1988) interfaced several existing packages with a GIS to produce a system with inductive learning capabilities which they used to model the distribution of kangaroos across Australia. Haslett *et al.*, 1990, recently reported a prototype statistical package for spatial data.

PART I. ESTABLISHING THE ENVIRONMENT GIS

This study coincided with a study of buzzard distribution and habitat use, conducted by Graham Austin, in the same area of mid-Argyll . We collaborated on all the elements of the work described in this section, namely acquiring or producing the digital environmental data and establishing the GIS. In addition, some of the programs used in Part II were jointly written, often with assistance from Tony Ibbs (Laser-Scan Ltd./Department of Topographic Science, Glasgow University). All joint work was undertaken side by side: we did not assume separate responsibility for different elements of the process.

DATA CONSIDERED FOR INCLUSION

Separate themes within the GIS used in this study, for example a vegetation map, are referred to as layers. A layer may be composed of multiple coverages (maps). Features from separate layers may be overlaid and stored as a new layer.

Prerequisites

A GIS is only as good as the data on which it is based. Each potential layer of data was assessed on five criteria:

1) the information must be biologically relevant to ravens

2) it must be available for large portions (if not all) of the study area, to a uniform standard at a scale of sufficient precision

3) it must be available in, or capable of being transferred to, a digital format

4) as far as possible, layers should explain separate aspects of the ecological landscape

5) preference was given to data sources available for other areas of the Scottish/British uplands to enable extension of findings in this study to be readily applied elsewhere.

Field data included: Ravens

Much of the data collected for ravens and considered in this part of the study were based upon nest locations. These were located on 1:50,000 scale Ordinance Survey maps to a precision of 100m, enabling digital maps to be prepared. When nests were not found (seven sites), the point of reference for the territory was assigned to the centre of the 500m Ordinance Survey grid square where raven activity was focused.

Field data not included: Large mammal carrion

A great deal of effort was put into trying to find methods of counting or estimating sheep and deer carrion in areas large enough to be included in this analysis. These were largely unsuccessful. Details of this work are not included in this thesis, but the reasons for rejection are summarised here as follows: 1) it was not physically possible to obtain estimates within confidence limits sufficient to spatially define even broad classes of projected variation in carrion supply over large enough areas of ground; 2) conditions at a very local scale appeared to influence more strongly the abundance and availability of carcasses than the broader terms of ecological reference, such as habitat or altitude, which I wished to consider; and 3) the cost in both time and money to obtain such data would make it unlikely to be available for other areas .

Previously published sources included

Landscape

The shape of the land is conveniently represented in two dimensions as contours of altitude, and outlines of coast and other water bodies. These are available in published Ordinance Survey maps of Britain: 50m contours at a scale of 1:50,000 were considered to be an appropriate level of precision for the present study. All 50m contours together with boundaries of sea, fresh water lochs, and rivers >5m across were digitised from the 1:50,000 scale Ordinance Survey maps. A separate coverage of cliffs and waterfalls (often landscape features too small for inclusion on 1:50,000 maps, but which may have been important to ravens) was obtained from 1:25,000 scale Ordinance Survey maps.

Human disturbance

The location of buildings and public metalled roads was considered a good indicator of potential human disturbance. These were available to a uniform standard from the 1:50,000 scale Ordinance Survey maps; however it was not possible to distinguish between deserted buildings and those still in use.

Vegetation

Maps of upland vegetation, prepared by Dr. P. Haworth (Glasgow University) and assisted in the field by Dr. D. Horsefield (Nature Conservancy Council, now Scottish Natural Heritage), were available for some parts of the study area at the time this analysis was done, and were included in the GIS. These were derived from interpretation of 1:24,000 scale aerial photographs taken on behalf of the Scottish Development Department in June and October, 1988. Interpretations were checked in the field by P.H. in two areas; south-east Mull and parts of north Lorn. These maps were actually prepared for another study, but for this one were inadequate because: 1) many parts of the study area remained unmapped; 2) forestry blocks were mapped from the boundaries given on Ordinance Survey 1:50,000 scale maps and gave no indication of variations in the fragmentation, the amount of open ground or the closure of the canopy within blocks; 3) boundaries of agricultural land were taken from field and fence lines shown on 1:25,000 scale Ordinance Survey maps rather than actual land use or vegetation; and 4) overall, the precision was considered too coarse for inclusion in analysis except where checked with field survey. However these data were a valuable source of reference for classifying satellite images.

As a further aid for classifying satellite images, 168 patches of distinct vegetation were drawn onto 1:50,000 scale Ordinance Survey maps in the field, during the summer of 1989, by myself and G.E. Austin.

Satellite remote sensing of land cover

Taking into consideration the enormous difficulties in producing a vegetation map of sufficient detail and coverage for this study, based on field survey, the use of classified, remotely sensed image data was a viable alternative. Two recent Landsat 5 images were available for the correct time of year which, when combined,

covered most of the study area. The additional cost and effort to obtain coverage for the areas not covered by these images (such as Tiree and north Mull) were beyond the scope of the project.

Previously published sources not included

Solid geology

This information was available on paper maps (sheets for Tiree and Argyll) for the entire study area from the British Geological Survey, with 1:100,000 being the most reasonable scale. Though these maps were digitised and initially included in the GIS, they were withdrawn from the analysis after digital terrain modelling revealed that most of the variance in the landscape shown by solid geology appeared to be accounted for by the terrain, elevation and slope, which were of more direct relevance to ravens.

Climate, soil, and land capability for agriculture and forestry

This information was available in the form of paper maps for the entire study area from the Macaulay Institute for Soil Research, Aberdeen (1982) at a scale of 1:250,000. In addition to this scale being too coarse for compatibility with other layers, soil and land-capability maps are ultimately derived mainly from field surveys of vegetation in combination with terrain, and thus represent a duplication of data within the GIS. Climatic maps were available at a scale of 1:625,000 (Map series: Assessment of Climatic Conditions in Scotland) from the Macaulay Institute for Soil Research, Aberdeen, published in 1970. However such maps are derived from mathematical formulas based on altitude and distance from the coast, again being features which were already included inherently in the GIS.

Sheep and red deer numbers

Red deer counts are available for selected estates throughout the Highlands, made by the Red Deer Commission. However, coverage in the study area was very limited and was not included. Yearly parish sheep numbers, recorded by DAFFS, are held on computer at the Edinburgh University Computer Centre (EUCC). These records are translated into a digital array of the average number of sheep per square km, based on the amount of land suitable for sheep within the parish. Since parishes are large in mid-Argyll, much local

variation was obscured by the method of calculation of sheep density and the database gave no indication of the proportion wintering on the hill. In addition , EUCC recommend that these data are not used below a resolution of 5km, which was too coarse for inclusion in the GIS. Thus the database was unlikely to be a good indicator of carrion supply.

THE ENVIRONMENT GIS

Equipment

I used Laser-Scan Ltd.'s "LAMPS" mapping software (Laser-Scan Ltd., 1989 & 1990) and "HORIZON" GIS versions 1.1, 1.2 and 1.3 (Laser-Scan 1991 & 1992) running in DEC WINDOWS on a DIGITAL 3100 VAX workstation located in the Department of Topographic Science, Glasgow University. The workstation was connected by Ethernet to the Glasgow University central VAX cluster for storage with a local disk available for page and swap files. GIS data were stored on the latest version of the INGRESS relational database system mounted on the VAX cluster. Macros (custom programs which can use the features of LAMPS and/or HORIZON) were written in Laser-Scan's LITES2 language, version 3.4.

DATA CAPTURE

Digitising maps

With the exception of raven nest locations, which were stored as text files of grid locations, and satellite imagery, which came in digital format, all other information needed to be digitised. Paper maps were digitised on a PC clone linked to a large format digitising tablet, using MAPDATA digitising software, located in the Department of Topographic Science, Glasgow University. The precision of the digitiser was to 0.3mm, which represented 15 metres on the ground when digitising 1:50,000 scale maps. Digitised coverages were converted from the MAPDATA format to Laser-Scan internal feature format (IFF; vector format) using a custom program (Ibbs, 1990 unpublished). Location of the data was stored by reference to the Ordinance Survey National Grid of Great Britain. Separate coverages of the same feature (e.g. contours) were combined into a single coverage using the Laser-Scan procedure **imerge**.

Ten figure grid references were used to locate raven sites. These were incorporated into the GIS and each given a unique identifier which would allow data from other layers to be referenced to particular sites.

REMOTE SENSING OF LAND COVER

Even though Landsat orbits a specific area every 16 days, only four images of the area were available which were not obscured by cloud. Of these, two were suitable as they had no snow cover and were largely free of cloud . The first image, acquired on 17th June, 1987, extended from the west coast of Mull over c70% of the study area, but did not cover the eastern 30%. Initial processing of this image was conducted at the Institute for Terrestrial Ecology, Monks Wood, Huntingdon, prior to the acquisition of the second image on 2nd May, 1990. This image covered the entire study area, but suffered from c10% very thin cloud distortion, in a continuous block located in the north-west corner of central Mull. Processing of the May, 1990 image, and final processing of the June 1987 image, were conducted in the NERC Computer Centre at the British Geological Survey, Edinburgh. Both establishments operated the same image processing systems: International Imaging Systems Inc. (I.I.S.) Digital Image Processing Software (I.I.S., 1989), running on a Model M75 processor with a VAX host central processor.

Classification procedure

The I.I.S. software is made up of a large number of procedures to perform operations on the image. In the following section, the names of I.I.S. procedures used are highlighted in **bold**.

Geometric correction by "rubber sheet warping", to correct for errors due to the perspective of the sensor optics and Earth curvature, was performed on the June '87 image by staff at ITE Monkswood prior to our arrival. This was done by simultaneously locating many identical features both on the image and on the 1:50,000 scale Ordinance Survey maps which were placed on a digitiser connected to the image processor. The resulting control point file was used by **c'cpwarp** to warp the image so that it was in a flat plane and with coordinates registered on the Ordinance Survey National Grid. The image was trimmed to exclude unwanted areas not n

the study area and restricted to Landsat TM bands 3,4, and 5, which we were advised would provide the best combination of wavelengths for the purposes of vegetation mapping.

Jones and Wyatt (1988) recommended that, in rugged terrain and areas where vegetation is predominantly heterogeneous at the scale of a pixel, as was the case in mid-Argyll, then unsupervised classifications are likely to produce the most satisfactory classifications. However, on advice from ITE, we first attempted a supervised classification of the image. During late summer of 1989, 168 polygons of distinct vegetation cover were drawn onto 1:50,000 scale Ordinance Survey maps in the field. These were digitised on to the image at ITE to serve as a basis for classification. A series of attempted classifications all produced poor results, with low predicted confidence in the majority of classes and, using our knowledge of the area, obvious misclassifications. This was due to most ground control polygons containing a too heterogeneous mixture of pixels: for example, a polygon described in the field as mature conifer forest plantation may actually contain many small open grassy areas or patches of scrub and birch. Additional sources of error arose from the ruggedness of the terrain: it was not possible to obtain a sufficient number of ground control polygons in every possible orientation and slope, features which greatly affected reflectance. Consequently, we adopted unsupervised techniques in further attempts at classification, which took place after the acquisition of the May '90 image, at BGS, Edinburgh.

The May'90 image (bands 3,4, and 5) was processed first. Areas of the image outside the area of interest were clipped out leaving a rectangular sub-scene 4,000 x 2,000 pixels in size. We did not have access to a digitising tablet to obtain ground control points for warping. Instead, the procedure **m'gcp'virtual display** was used to simultaneously display both the May'90 image and corrected June'87 images in virtual roam mode. 21 pairs of identical points were located interactively on each image to produce a control point file. This was used by **c'cpwarp** to rubber sheet warp the May'90 image and register it on Ordinance Survey National Grid coordinates. A sub-scene from the May'90 image is shown in Figures 5.1.

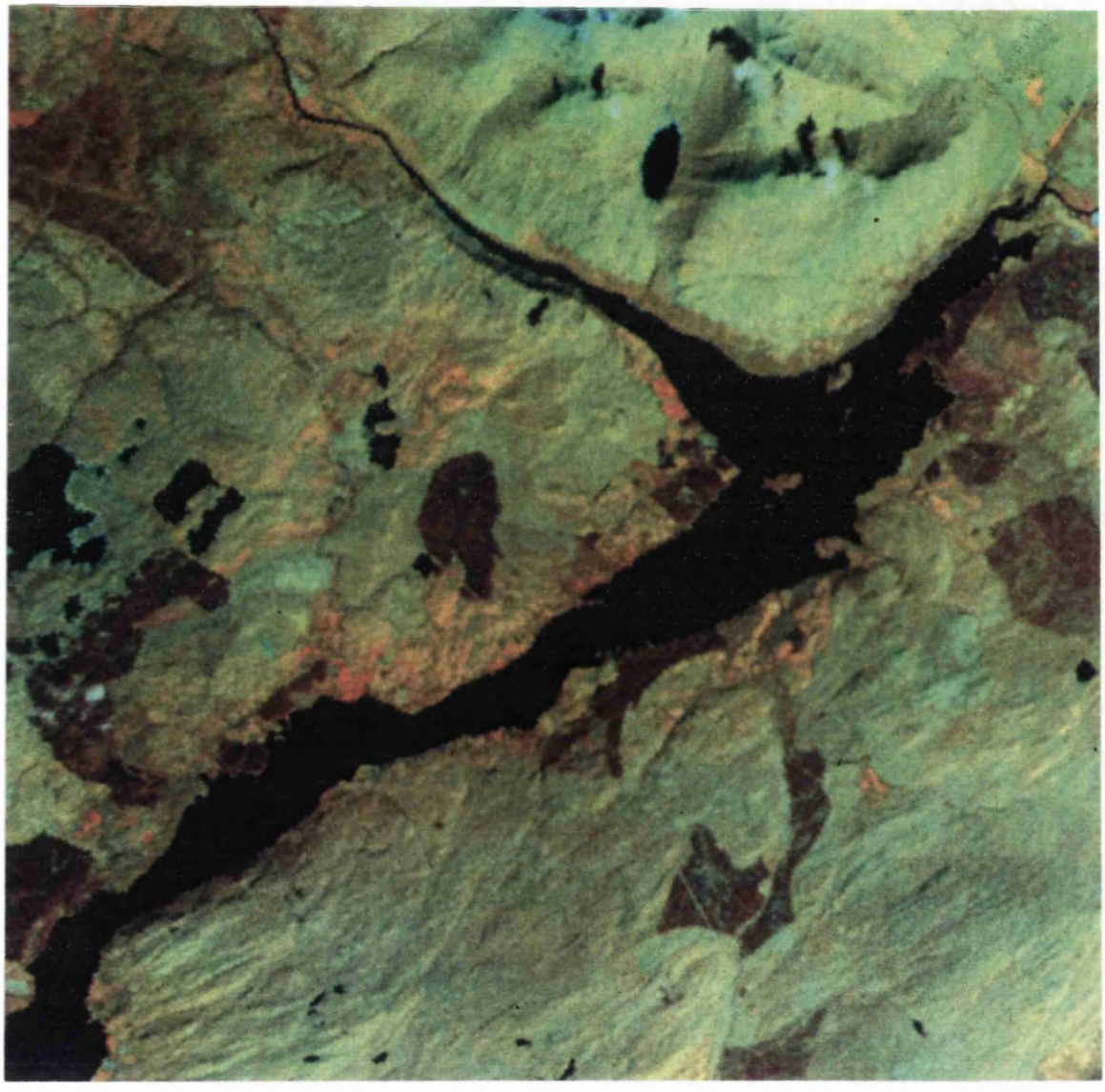


Figure 5.1 Unclassified display image of north Loch Awe taken by Landsat 5 Thematic mapper, 2nd May, 1990.

512 x 512 pixel subscene (15.36km x 15.36km)

Water appears as black, mature conifer plantation as dark red, improved agricultural fields as orange, and semi-natural grasslands and moorland as mixtures of greens and blues. Note the small clouds and shadow on Ben Cruachan in the top centre of the image.

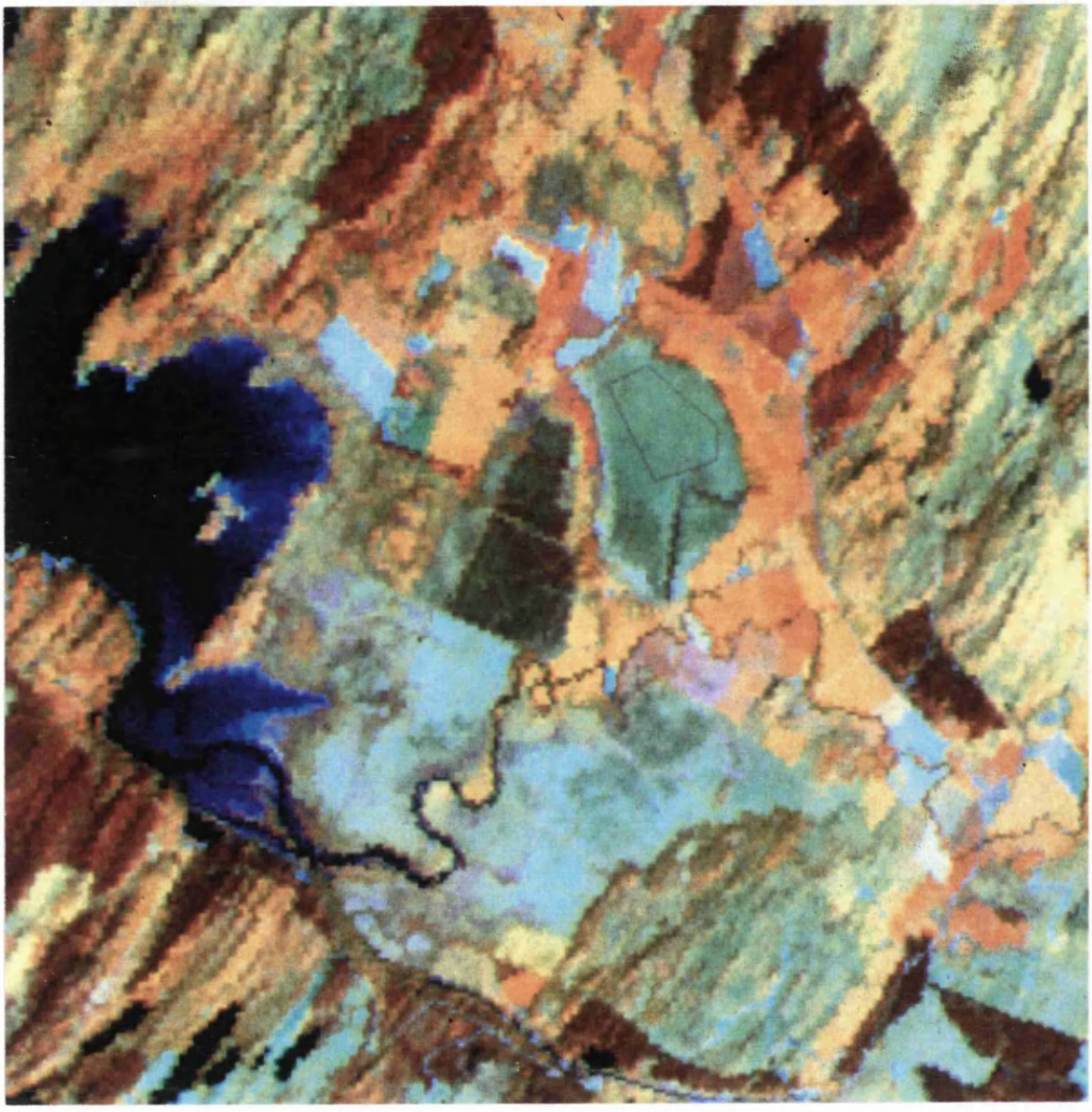


Figure 5.2 Zoomed in view of unclassified display image of Crinan canal area of mid-Argyll taken by Landsat 5 Thematic mapper, 2nd May, 1990.

Individual pixels representing 30m x 30m on the ground can be seen.

Deep water appears as black, shallow water as violet, mature conifer plantation as dark red, improved agricultural fields as orange, and semi-natural grasslands and moorland as mixtures of yellows greens and blues. Note the vector polygon laid within the solid green area in the centre of the image. This was an area of bog mapped in field survey used as an aid to classification The Crianan Canal can be seen in the bottom centre of the image.

Individual pixels may have a reflectance largely affected by some feature not representative of the land-cover in that area, for example a single tree, parked car or building. **C'convolve** was used to perform a Gaussian transformation of the data array, using a five by five kernel shown in Figure 5.3. The value of the central pixel in the matrix is weighted according to its neighbours. This causes individual pixel values to migrate towards those of its neighbours, which is useful in reducing noise by smoothing the frequency distribution of pixel intensity in each waveband, but preserves boundaries.

0.0025	0.0125	0.02	0.0125	0.0025
0.0125	0.0625	0.10	0.0625	0.0125
0.02	0.10	0.16	0.10	0.02
0.0125	0.0625	0.10	0.0625	0.0125
0.0025	0.0125	0.02	0.0125	0.0025

Figure 5.3. Kernel file Gaussian weightings applied to pixels.

For each waveband the new value of the central pixel (double boundary) was calculated as

$$\sum \text{ kernel value x pixel intensity.}$$

In an unprocessed image, the full range of the radiation recorded in each waveband is scaled from a value of zero (lowest reflectance) to 255 (highest reflectance). However, most of the values of interest are not at these extremes. Image enhancement techniques were employed to remove unwanted pixel values from each end of the distribution and proportionately rescale the remaining values over the range 0 - 255. This spread the values of interest across a greater range allowing increased differentiation amongst potential statistical groups. Using the recommended values for the **high-clip** option in **c'scale**, the pixels in the upper 2% of the distribution in

each were clipped out: this effectively removed the few existing very bright pixels, which almost certainly did not relate to vegetation (e.g. small patches of snow, tin-roofed sheds etc.) and which skewed the distribution. At the low end of the distribution (dark objects), there was much overlap between features of interest and unwanted features, and thus potential sources of confusion. Level slice procedures were used to examine the distribution of pixel values in relation to ground cover at the low end of the scale on each waveband. Level slicing, also known as density slicing, allows the operator to view the image with different regions of the pixel value range in each waveband coloured differently. Aided by our knowledge of the area, vegetation maps, and locations of ground truth polygons, many ground-cover types were apparent even in the unprocessed image: deep and shallow water, pre-thicket and mature forestry, open grass and moorland, wet bog, and agriculturally improved pasture. Areas in deep shade were also clearly visible. The I.I.S. procedure **level_slice** cannot be used over large areas: the largest sub-scene possible was 512 x 512 pixels (15.36 km x 15.36 km). Five sub-scenes (display images) were defined which each contained, as far as possible, the range of pixel values and terrain found across the entire image. **Level_slice,** in increments of one, beginning at zero, was performed on each display image until a reasonable compromise was reached between excluding unwanted regions of the distribution and yet leaving in sufficient values for subsequent classification. An illustration of level slicing is given in Figure 5.4.. This was a trial and error procedure involving a great many runs, and checking that the results obtained from one display image were applicable to the others. The main source of confusion was between shade and shallow water overlapping with values for mature forestry plantation. Values to be cut out using **low-clip** were established as follows:

Band 3: pixel values 0-22 (lower 8.6% of the distribution). This removed 100% of shallow water, c50% of areas in shade and all mature forestry.

Band 4: pixel values 0-40 (lower 15.7% of the distribution). This removed 100% of areas in shade and all areas of shallow water but stopped just short of removing pixels of mature forestry. At pixel value 41, the first forestry pixels were lost.

Band 5: pixel values 0-50 (lower 19.6% of the distribution). This removed 100% of shade, 100% of shallow water and 100% of mature forestry.

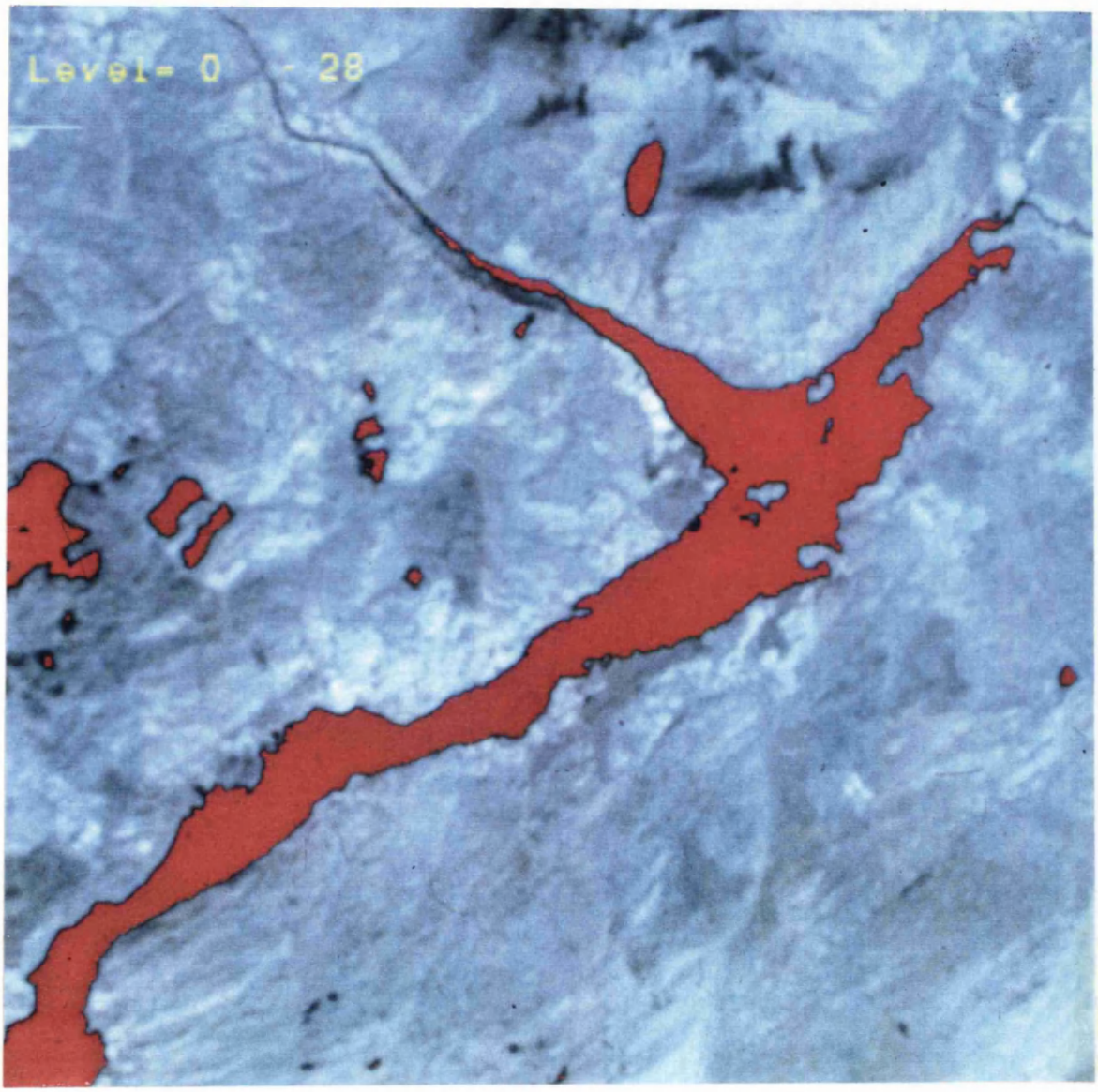


Figure 5.4 Level slice applied to north Loch Awe display image, illustrated in figure 5.1, from Landsat 5 Thematic mapper image, 2nd May, 1990.
512 x 512 pixel subscene (15.36km x 15.36km)
Waveband 3; pixel values 0-28 are shown in red, other values in grey. The coloured range includes only those pixels in water. As areas of water were already known these could be clipped out of this waveband using this procedure and allow reflectance values to be rescaled.

With **high-clip** and **low-clip** values now established, **c'scale** was used to remove these portions of the distribution from each waveband and rescale each across the range 0-255 for the entire image. An unsupervised classification was then run. Again this could only be performed on 512 x 512 pixel display images. Procedure **m'cluster_class** was used to classify one display image which was most representative of the entire area, with the full range of land cover and terrain present. In this procedure the operator chooses the number of starting classes and number of iterations which the clustering algorithm may employ to produce a classification. Seed points for the first iteration are placed in the centre of equal area sections of the frequency histogram of pixel values, determined by the number of starting classes used. Subsequent iterations cause the loss of some of these classes. We employed the **extrema=yes** option to force the iteration to work from the ends of the distribution towards the centre, which reduced the chance of outer seeds being lost. This was important in our case since reflectance values for many of the land cover classes we wished to distinguish were located close together towards the lower end of the tails, and we wished to split this area as much as possible. Specifying this option caused a high loss of classes in the initial iteration, so we chose a much higher number of starting classes than we ultimately hoped to produce. Thirty iterations were sufficient to produce a stable classification. Since it was anticipated that categories would be merged in the process of final classification on the GIS, we produced a classification with an excessive number of categories at this stage. A stable classification of 21 classes was produced (from 40 starting classes). Final statistics from the classification were obtained and placed in the prepare file **class.prep**. This file was used in the procedure **m'v'mdclassify** to apply these statistics to the whole image and produce a 21 class, classified image. The classified image was closely inspected to ensure a good visual fit with vegetation maps, our ground control polygons, and knowledge of the area.

Whilst the classification appeared very good, it was apparent that many pixels remained unclassified, usually on the boundaries of homogeneous blocks or within heterogeneous land cover types such as forestry, due to pixel mixing. **M'v'mdclassify** is a minimum distance classifier, which ensures that each pixel is assigned to the class to whose mean it lies closest, with a default setting of ±2 standard deviations. It was possible to force the unclassified pixels into classes by increasing the tolerance to >2 s.d. . This did not alter the classification of

those already classified, but included previously unclassified pixels into their nearest class. The entire image was classified using **class.prep** with a tolerance of ±5 s.d. . Although there was a lower degree of confidence in the classification of some pixels using this tolerance, it was obvious upon visual inspection that the vast majority had been placed into classes that we would have expected them to be for reasons other than their reflective signature, such as spatial proximity to pixels classified with high confidence. For example, formerly unclassified pixels on the boundary between two homogeneous blocks were assigned to one of those blocks, and pixels formerly unclassified within forestry were placed in that class. Some pixels remained unclassified, as they were >±5 s.d. away from centres of classes.

The classified image at this stage was still overly complex for our purposes. We smoothed the image using **m'v'mode_filter** applying a model filter using a 3 x 3 kernel (weighting applied to each cell = 1) using the **isolated** qualifier. The object was to reclassify those individual pixels which were classified unlike any neighbouring pixels to be the same as the majority of pixels surrounding them. This is illustrated below in Figure 5.5. If a pixel was unique in an area, this was more likely to be an artefact of the processing or a small feature in the landscape of no interest to us.

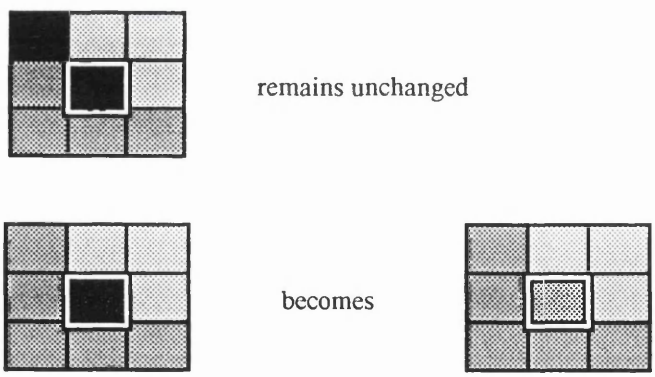


Figure 5.5. Effect of reclassifying unique pixels with 3x3 modal filter.
Pixel under scrutiny shown in centre of matrix with double boundary.

No further processing of the image was undertaken on the I.I.S. system. An identical procedure was adopted for the June'87 image. However this did not require extensive level slicing and defaults were used. Ultimately a

classified image with 17 classes was produced. A sub-scene from the 21 class May'90 classified image is shown in Figure 5.6.

Import of classified images into the GIS

Hereafter, the Laser-Scan LAMPS and HORIZON procedures, rather than I.I.S. procedures, are highlighted in **bold**. The images were converted from I.I.S. system 600 format to its 575 format to be compatible with Laser-Scan conversion programs. These data were then converted to Laser-Scan raster format (DTI) using **dtmconvert**. **Dtitrans/descriptor** was used to convert data headings and define map projection, spheroid and local origin for the GIS.

Patching together classified images within the GIS

A window corresponding to the smallest rectangular area containing pixels affected by cloud on the May'90 layer was removed from the June'87 layer using procedure **dtitile** and saved as a new layer. This area was made void in the May'90 layer using **dtitile**. This layer and the window from the June'87 were combined using **dticombine** into the satellite derived vegetation raster map to produce a complete coverage of the study area unaffected by cloud. Examination of the boundary between the two images showed an extremely good fit between apparently equivalent classes, although one class in the June'87 classification had been split into two in the May'90 classification.

Final classification within the GIS

The satellite derived vegetation raster map was overlaid with the vector layer of water body boundaries in HORIZON. This revealed an extremely good fit between the boundaries of water bodies produced by classification of the satellite images and those derived from digitising Ordinance Survey maps, and confirmed that orientation and location of the image in the GIS was correct. By overlaying the satellite derived vegetation raster map with the vector map of vegetation derived from aerial photographs, comparison with ground control polygons on paper maps, and our knowledge of the area, it was clear that several classes of land cover had been correctly assigned at this stage and needed no further clarification. These were:

deep water, away from the shore

shallow water, near the shore or in shallow lochs

mature forestry plantation, characterised by a closed canopy

pre-thicket forestry, with spaces between young conifers containing a thick herb and grass layer and young birch tree scrub. This class did not contain new-plantation forestry with very young trees.

agriculturally improved pasture

However, areas of deciduous and mixed deciduous/coniferous woodland were inconsistently classified in areas of the coverage derived from the May'90 image. In the portion of the coverage derived from the June'87 image, one class was consistent with those areas marked as deciduous woodland on 1:50,000 scale Ordinance Survey maps, but mixed woodland was inconsistently classified, although there were few patches of either of these types of land cover in the area. It is not surprising that deciduous woodland was not detected as a distinct class in the classification of the May'90 image since, at this time of year, most of this growth is still in bud. Mixed woodland was obviously too heterogeneous for clustering to detect as a distinct class. The boundaries of these two vegetation types given on 1:50,000 scale Ordinance Survey maps (revised 1984) were known from our fieldwork to be reliable and accurate, and little if any change had taken place in the intervening years. Consequently, boundaries were digitised from 1:50,000 scale Ordinance Survey maps directly into Lites2 as a single IFF (vector) format coverage. Woodland vectors were converted into polygons using **ilink/merge** to merge overlapping vectors, **ilink/break** to break vectors at junctions, **ilink/structure** to reformat the topology of the data set and finally **ipolygon/polygons** to produce closed polygons containing woodland. This coverage was converted to raster (30m pixels) using **i2grid** and patched into the satellite derived vegetation raster map using **dticombine,** so that the new pixel value (for deciduous or mixed woodland) replaced the previous value.

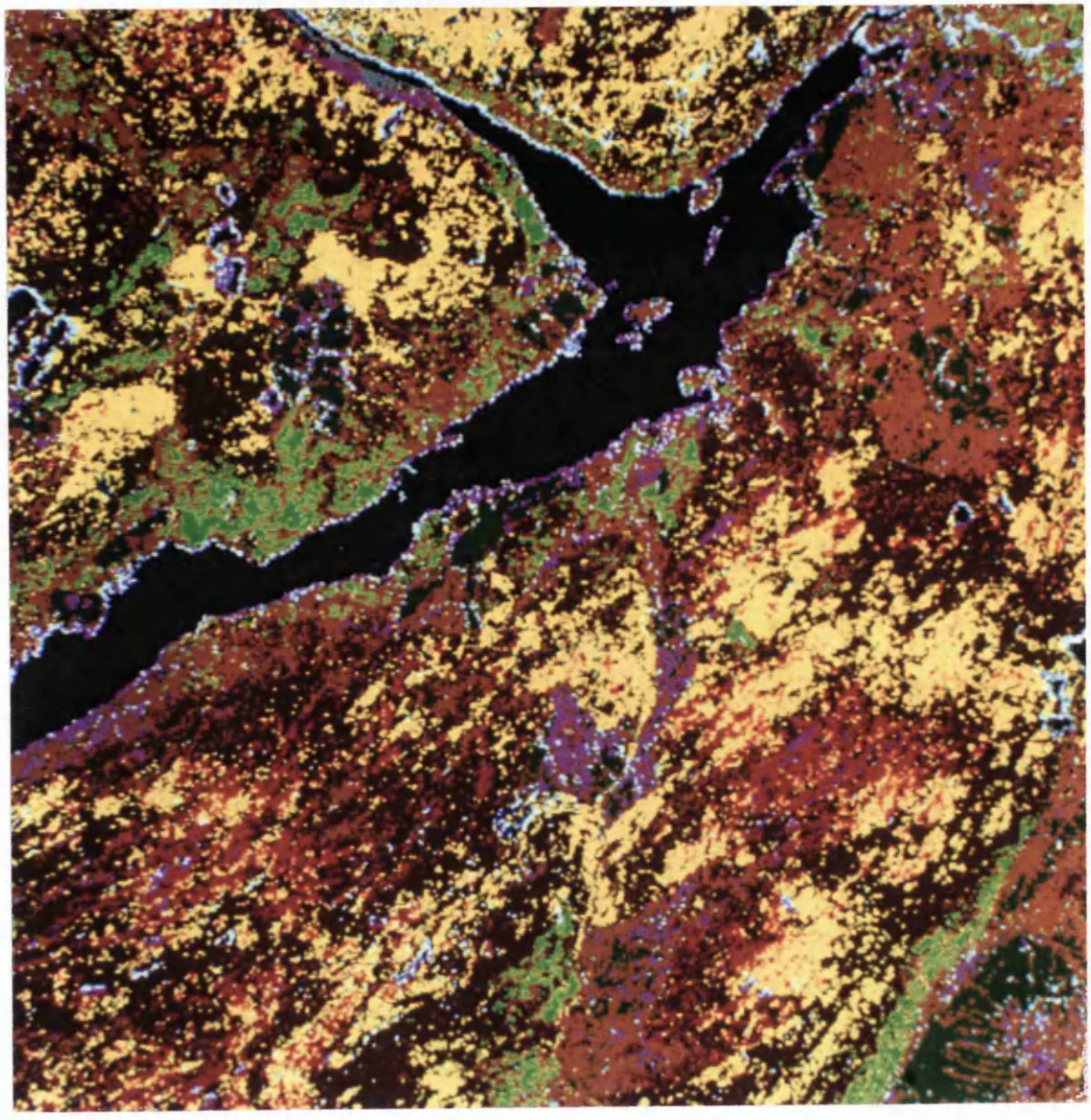


Figure 5.6 Landsat 5 Thematic mapper image, 2nd May, 1990 in 21 classes derived by unsupervised classification.
512 x 512 pixel subscene (15.36km x 15.36km)
See text for details of classification procedure.

Five classes in the satellite derived vegetation raster map, plus void pixels (areas outside the image but contained in the coverage) were merged into one class defined as 'unclassified'. These corresponded to pixels imported into the GIS as unclassified, void , and four classes of land cover representing mixtures of shade, rare land cover types, towns or interference remaining after initial processing on the I.I.S.. The latter were considered best classed as unknown rather than risk misclassification.

Using the satellite image, we could not distinguish between fresh and salt water. This was an important consideration for ravens since the sea coast is a productive foraging area which may have influenced territory quality. Consequently, vector maps of water boundaries were converted to fresh and salt water polygons, converted to a 30m raster coverage and patched into the satellite derived vegetation raster map using the same procedures as for woodland, replacing pixels previously classed as water with classes for salt or fresh water.

This, at this stage, water, woodland, forestry, and improved pasture were considered correctly classified. The large remaining areas, comprising open hill ground, required a more detailed analysis to produce a corrected classification. The vegetation in these upland sheep walk and deer forests present problems for vegetation mapping by any method, as communities tend to grade into each other on a continuum rather than to form wel delineated blocks of homogeneous coverage (see Brown *et al.*, in press a, in press b; Thompson and Brown, 1992). We wished to derive a classification of these open hill vegetation communities at the level shown in the vegetation maps, namely: blanket bog (dominated by *Calluna/Eriophorum*/mixed grasses); heather moorland (dominated by *Calluna*); upland perennial grassland (typically *Agrostis* dominated); and wet heath (*Molinia* dominated). Not only was it unlikely that we could have derived a classification which disinguished upland vegetation communities at a finer scale than this with confidence, but, for the purposes of the intended analyses, this level of mapping was considered adequately detailed.

An objective method of sampling points simultaneously on the vegetation map and the satellite derived vegetation raster map was developed. Although this procedure could have been automated, interactive querying was considered more efficient for this once only application. The satellite derived vegetation raster

map was displayed in HORIZON and overlaid with the vegetation map derived from aerial photographs. Using the facility **show grid**, a 200 m grid was superimposed upon this display. Considering only those areas of the vegetation map known to have been checked by field survey, we identified all 200m grid cells lying within polygons categorised by the survey as homogeneous blocks of open hill vegetation. To minimise edge effects, we excluded cells lying less than one complete cell within the boundary of the polygon. The centre of each 200m cell remaining was identified and the value of the pixel underlying this point in the satellite derived vegetation raster map was interactively obtained using the function **show $imagevalue**. Results were sent to an ASCII text file giving vegetation category and satellite class for each point. We were able to extract 2702 points: from the four open hill vegetation categories selected, 14 classes of the classified image were recorded. No points recorded forestry, or, of course, woodland or water, since these were derived from the same source in both cases. Three points were removed as these corresponded to areas previously determined to be unclassified. The resulting correspondence matrix is shown in Table 5.1. Landsat classes are shown labelled alphabetically in the order they were classified by I.I.S.. There were several potential sources of error in the correspondence matrix. As discussed previously, open hill vegetation of these types are usually found grading into each other on a continuum, and because of this, the delineation of boundaries between communities was a subjective decision which may have varied over areas mapped in a way which assigning boundaries by statistical analysis of reflectance did not. Secondly, errors may have occurred in transcribing boundaries detected from aerial photographs (1:24,000 scale) by hand onto smaller scale (1:50,000) paper maps. These sources of error were minimised by sampling away from vegetation polygon edges, but would not have been completely overcome. Finally, small patches of vegetation (<c400m^2), which differed from the surrounding vegetation, were not included on the vegetation maps, but these were often detected by the finer scale of Landsat pixels. Patches of distinct vegetation of this size, such as grassy patches in heather moorland, were common in open hill communities in the study area. This source of error was minimised by the Gaussian transformation and modal filtering of the satellite image, but patches larger than two pixels which were very distinct from their neighbours in reflectance would have persisted.

Landsat Class	Blanket Bog	Heather Moorland	Upland Perennial Grassland	Wet Heath
A	33	5	15	0
B	239	74	35	4
C	59	25	81	81
D (agric. grass)	0	0	13	0
E	41	15	41	0
F	255	65	111	32
G	80	22	80	126
H (agric. grass)	0	0	46	0
I	73	13	122	6
J	54	1	4	86
K	50	25	95	40
L	29	8	49	73
M	8	8	103	8
N	11	0	67	188

Table 5.1 Correspondence matrix of classes derived from the classification of the Landsat image and four categories of open hill vegetation shown on vegetation maps derived from interpretation of aerial photographs.
Categories D and H had already been identified as agriculturally improved grassland, the identity of other Landsat classes was unknown.

Two classes from the satellite derived vegetation raster map were found at locations given as open hill ground which previous investigation showed to best represent improved agricultural grassland (D and H). In each case, they were found in areas mapped as upland perennial grassland. This was because particularly rich patches of this grassland closely resembled improved fields in reflectance signature. However both can be considered biologically similar, representing the same kind of vegetation community (short sward, rich perennial grasses), and thus no source of conflict in the intended analysis of ravens and habitat quality. Locations corresponding to Landsat classes D and H were therefore excluded from further analysis.

Other Landsat classes occurred in more than one vegetation category. Interactions between these were investigated by correspondence analysis using the SPSS PC+ ANACOR procedure with canonical normalisation. This allowed the relationship between two sets of nominal variables to be presented graphically in multidimensional space (SPSS Inc. 1990). The first two dimensions derived explained a total of 98.3% of the total inertia: dimension 1 accounted for 67.8% and dimension 2, 30.5% . A plot of the locations of vegetation categories and Landsat classes along these two dimensions is given in Figure 5.7. The first dimension represented the gradient from vegetation communities with a high heather component to those with deciduous grasses (heather moor and blanket bog to *Molinia* dominated sheepwalk) and the second dimension the gradient from dry, short sward perennial grasslands to wetter, bog and heath communities. This plot served as a basis for determining which Landsat classes should be merged and assigned to vegetation categories. However, this analysis was insufficient when considered in isolation as it did not take into account any spatial relationship between Landsat classes. For example, some classes were found frequently intermingled, indicating probable relatedness, or rarely together, indicating probable real differences. Consequently in assigning group membership, the correspondence matrix and plot were used in conjunction with a visual examination of the satellite derived vegetation raster map overlaid with the vegetation map derived from aerial survey.

Landsat classes J,G,L, and N were statistically grouped around wet heath. These classes were usually observed together on the classified image, and together closely conformed to the boundaries of wet heath. Classes E,I and M regularly occurred together in areas mapped as perennial grassland, and were statistically associated with this category on the correspondence plot. Blanket bog and heather were associated on the correspondence plot, as they were in the field, and were poorly separated by the statistical approach. Three classes, B, A, and F were clearly associated with these two categories. Boundaries of class B and polygons of heather moorland tended to coincide, and this class was dominant within these polygons. Class F tended to occur in areas not designated as heather but as blanket bog, although there was some overlap. Class A was relatively rare and tended to occur in proximity to class F. Class C was equidistant from all four vegetation categories on the correspondence plot but rarely occurred with classes assigned to wet heath. This class was most frequently

found mixed with classes assigned to blanket bog, especially class F. This also applied to class K, although it was statistically close to perennial grassland. It was likely that both C and K were intermediate between perennial grassland and blanket bog (either in reflectance or due to heterogeneity of habitat) and may have been mapped as either one or the other from aerial photographs using cues not available in image processing. Because of their spatial proximity with class F, both were associated with blanket bog. Landsat classes were thus combined according to Table 5.2.

Final classification of the corner of the image patched in from the June'87 image was performed by visual inspection of the boundary with the satellite derived vegetation raster map. The boundaries of polygons corresponded very closely across this boundary and classes in the June'87 window were renamed accordingly.

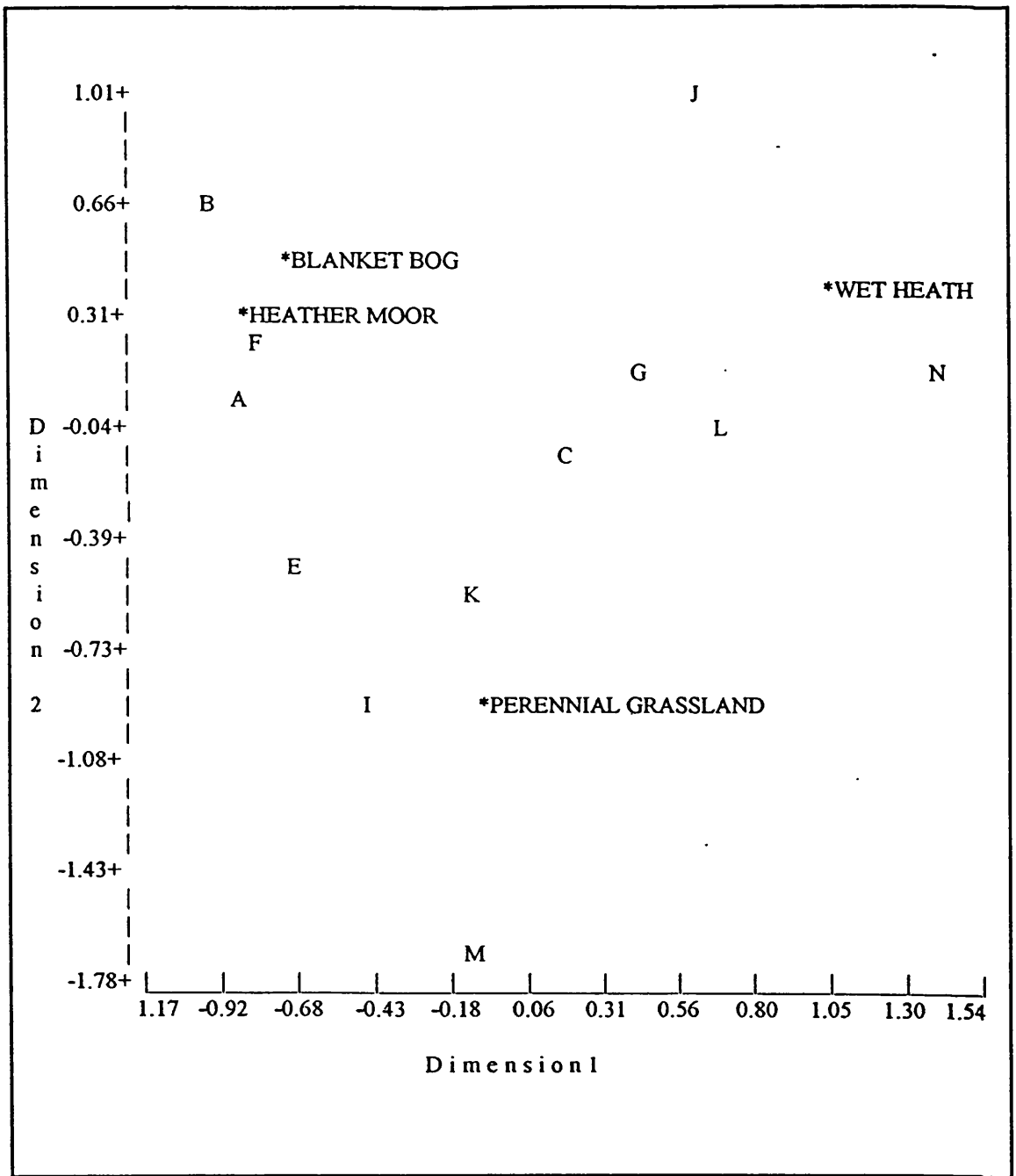


Figure 5.7. Correspondence plot (canonical normalisation) of vegetation categories and Landsat classes. Vegetation categories (from map derived from interpretation of aerial photographs with ground checking) named as mapped; Landsat classes (derived from unsupervised 21 class classification) shown as letters.

Landsat Classes	Description
B	Heather Moorland
A C F K	Blanket Bog
E I M	Upland Perennial Grassland
G J L N	Wet Heath

Table 5.2 Landsat classes corresponding to open hill vegetation categories

The 21 Landsat classes imported from the I.I.S. were thus merged to produce the following 12 class coverage:

1. unclassified
2. post-thicket coniferous afforestation
3. pre-thicket coniferous afforestation
4. heather bog
5. mixed bog
6. wet heath
7. rich short sward perennial grassland (mainly agriculturally improved fields)
8. perennial grassland
9. broad-leaved woodland
10. mixed broad-leafed/coniferous woodland
11. fresh water
12 salt water

It should be noted that areas of bracken *Pteridium aquilinum* were not identified in this classification, since in May, the fronds were only very small shoots and most of the previous year's dead fronds had disappeared. Bracken grew later in the season almost exclusively in areas classed as perennial grassland. Although during the period of raven breeding it was not present, and the land was classified correctly for this time, its presence at other times of the year may have affected the quality of the land for ravens. In the area considered from the June image, there were only very small patches of bracken and these were removed by the image smoothing

and filtering techniques available within I.I.S.. Areas newly planted with conifers were not differentiated from classes of heather or wet heath. However, at this stage of development, with very small seedling trees well dispersed in grass/heather, this is a correct biological classification. Correct classification of maturing plantations was possible with the up-to-date 1990 image. There was no new plant or pre-thicket afforestation in areas covered by the 1987 image.

DIGITAL TERRAIN MODELLING

Introduction

Physical features of the landscape, apart from land cover, can have a significant impact on the suitability of an area for animals. For example, for many species, suitable habitat lies within an altitude band; even though preferred land covers and prey may occur outside this band, climatic constraints render it unsuitable. Other animals demonstrate a preference for certain types of terrain: many species of breeding waders will not breed on slopes above 15° even though otherwise apparently suitable nest sites occur in abundance. For crag nesting species such as the raven and many raptors, the terrain will determine the availability of preferred nest sites. On a more general level, for animals with large home ranges local differences in topography may make important differences to the quality of habitat, even within the same altitude zone and land cover. For example, slope and aspect will determine the length and depth of snowlie, and slopes in shelter from prevailing winds may allow more or better foraging than in exposed sites. Measurement of terrain has in the past proved a cumbersome and time consuming task. Digital terrain modelling permits the extraction of many terrain variables from height contour data which are of potential use in habitat suitability modelling, with the additional benefit that the digital coverages produced may be easily integrated into a GIS.

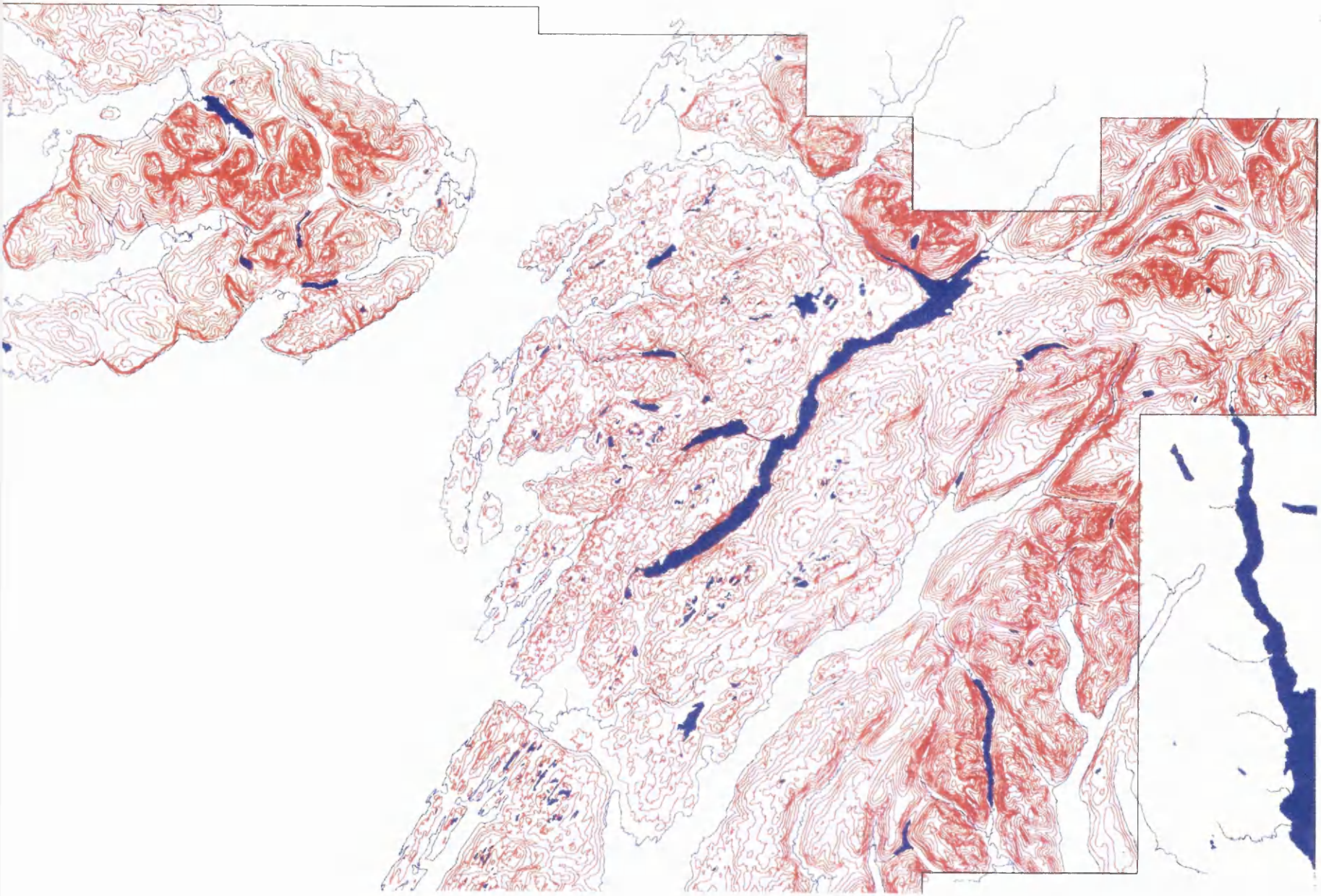


Figure 5.8. 50 metre contours digitised from 1:50000 Ordinance Survey maps.

Software

A complete vector coverage of 50m contours was digitised as described in Section 5.6a (Figure 5.8). From this, a raster map of altitude was derived using the Laser-Scan digital terrain modelling modules in **dtmcreate**. The raster map of altitude served as a basis for deriving three other layers of terrain information thought potentially relevant to ravens: slope, aspect and neighbourhood altitude range.

Classification procedure

The vector map of contours was combined with that of water bodies to create boundaries for the digital terrain model at the coast. The boundary of the area to be modelled was digitised into this coverage. Boundaries at coverage edge and coastlines were given an altitude of 1m, in effect creating a 1m "cliff". Due to the extent of the coverage, it was clipped into four, slightly overlapping quadrants. **Dtmcreate** modules **Trider** and **Triang** were used to produce a solid model of the landscape in each of these quadrants (Figure 5.9). **Triang** determined Theissien neighbours for each point in the complete data set of contour points (digitised points along contour lines). By joining neighbouring points around every point, a system of triangles was built up by Delaunay triangulation. **Trider** was used next to produce slope derivatives at each data point used in the triangulation. Finally, **trigrid** was used to transfer the altitude information onto a raster grid. The size of the grid (pixel size) was set to 100m; this was considered sufficient detail for the analysis, being close to the scale of the Landsat coverage, and yet not below the scale at which the contours had originally been digitised.

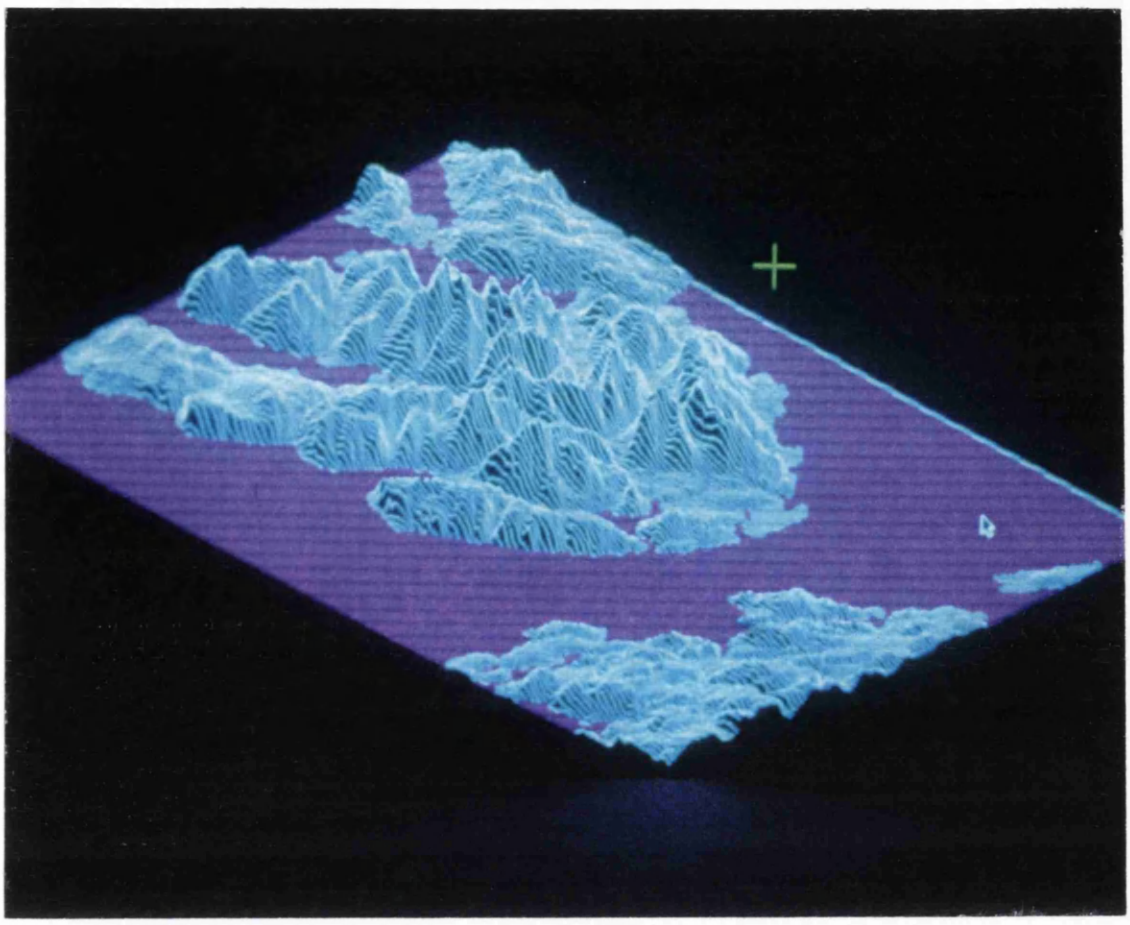


Figure 5.9 Solid model of landscape: Mull viewed from the south-east
Isometric projection with 3x vertical exaggeration.

Within HORIZON the four raster coverages were combined in one layer of altitude. This raster coverage served as the basis for producing slope, aspect and neighbourhood altitude range raster layers (100m pixels) using the surface analysis procedures in the **terrain** function. Surface slope was generated as the average gradient in a 3 x 3 matrix of altitude pixels to the nearest degree. Surface aspect was generated as degrees from North for each pixel. Neighbourhood altitude range (surface height analysis) was produced by calculating the maximum difference in altitude in a 3 x 3 matrix of altitude pixels. The range of values in this parameter within a region gives an indication of surface ruggedness independent of slope and altitude. For example in

Figure 5.10, terrain A has more slope but is less rugged than in B. Neighbourhood altitude range is referred to as 'ruggedness' from here onwards.

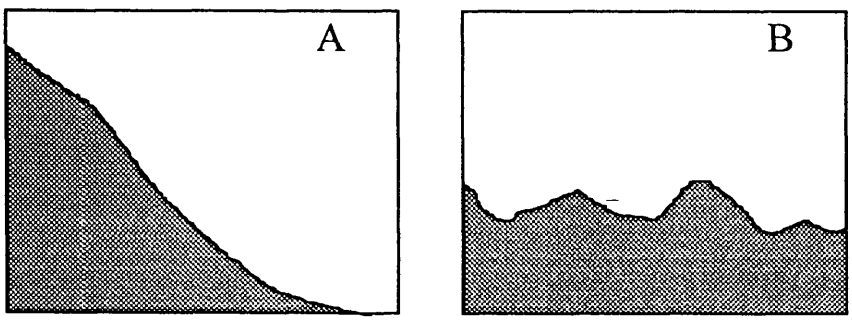


Figure 5.10. Schematic representation of the difference between slope and ruggedness
Cross section of two contrasting landscapes. Terrain A has more slope but is less rugged than B

The four additional terrain layers were produced by classifying terrain raster maps into the following categories using **dticombine**:

altitude in 100m intervals: class 1 = ≤100m
" 2 = >100m to ≤200m etc.

slope in 10° intervals: class 1 = 0° (flat)
" 2 = >0° to ≤10°
" 3 = >10° to ≤20°
" 4 = >20° to ≤30° etc.

aspect in 90° intervals: class 1 = 0° (flat)
" 2 = >315° to ≤360° and >0° to ≤45° (North)
" 3 = >45° to ≤135° (East)
" 4 = >135° to ≤225° (South)
" 5 = >225° to ≤315° (West)

ruggedness in 10m intervals: class 1 = 0m (flat)
" 2 = >0 to ≤10m
" 3 = >10m to ≤20m etc.

Areas of water were removed from all terrain coverages so that the pixel values related to land only by using the following procedure. The satellite derived vegetation raster map was resampled (using a modal algorithm) to 100m pixels using **dtitransform** to produce a new coverage whose pixels matched those in terrain raster coverages. **Dticombine** was used to reclassify classes 1-12 in this coverage as 'land', and classes 12 + 13

(fresh and salt water) as 'water', to produce a new raster layer with two classes, land and water. Each terrain coverage was merged in turn with this layer using **dticombine** to make void all pixels in terrain maps which were classed as water.

FINAL DATA LAYERS IN THE GIS

Thirteen layers were finally included in the GIS which were used in subsequent data-extraction and modelling:

1. Landsat derived raster coverage of land cover in 12 classes (30m pixels)
2. Contour derived raster coverage of altitude (100m pixels, in units of 1m)
3. Contour derived raster coverage of altitude (100m pixels, in 100m classes)
4. Altitude derived raster coverage of slope (100m pixels, in units of 1° from 0 to 90)
5. Altitude derived raster coverage of slope (100m pixels, in 10° classes)
6. Altitude derived raster coverage of aspect (100m pixels, in units of 1° from 1 to 360, with 0 = no aspect)
7. Altitude derived raster coverage of aspect (100m pixels, in 5 classes: 0 = no aspect; 1 = North; 2 = East; 3 = South; 4 = West)
8. Altitude derived raster coverage of ruggedness (100m pixels, in units of 1m, with 0 = flat)
9. Altitude derived raster coverage of ruggedness (100m pixels, in 10m classes)
10. Digitised vector coverage of human culture, with three features: A roads, B roads, and buildings
11. Vector boundaries of study areas digitised directly in HORIZON: main study area and four intensive study sub-areas
12. Vector points of raven sites, converted from grid locations.
13. Boundaries of water bodies and rivers.

Examples of data in vector and classified raster layers are illustrated in Figures 5.11 to 5.17

KEY FOR FIGURES 5.11 AND 5.12.

LANDCOVER CATEGORIES DERIVED FROM CLASSIFIED LANDSAT IMAGES

- Unclassified
- post-thicket coniferous plantation
- pre-thicket coniferous plantation
- *Calluna* bog
- mixed bog
- wet heath
- rich short-sward perennial grassland (mainly agriculturally improved fields)
- semi-natural perennial grassland
- broad-leaved woodland
- mixed broad-leaved/coniferous woodland
- fresh water
- salt water

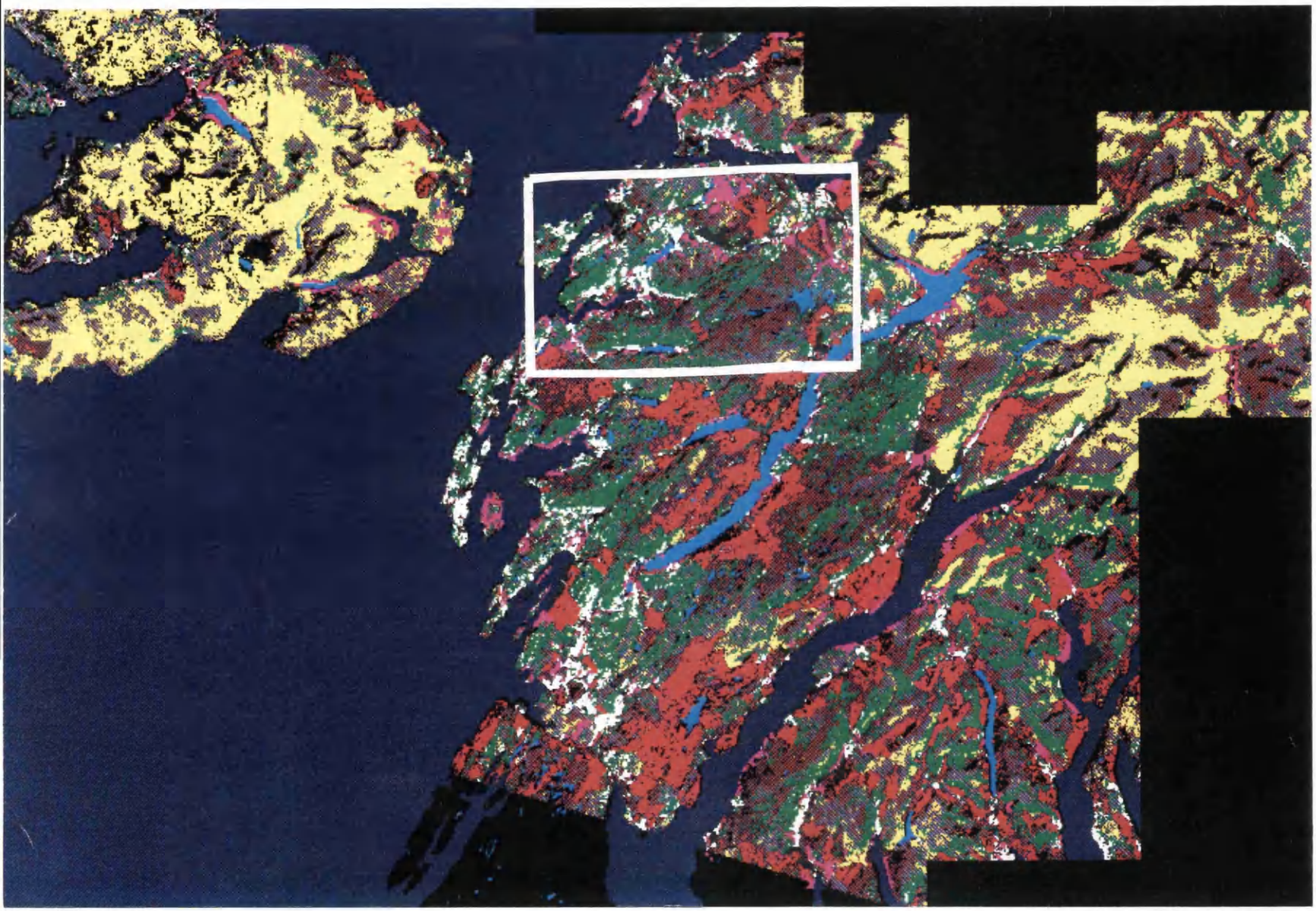


Figure 5.11 12 class land cover GIS layer derived from Landsat images. Windowed area shown enlarged in Fig. 5.12

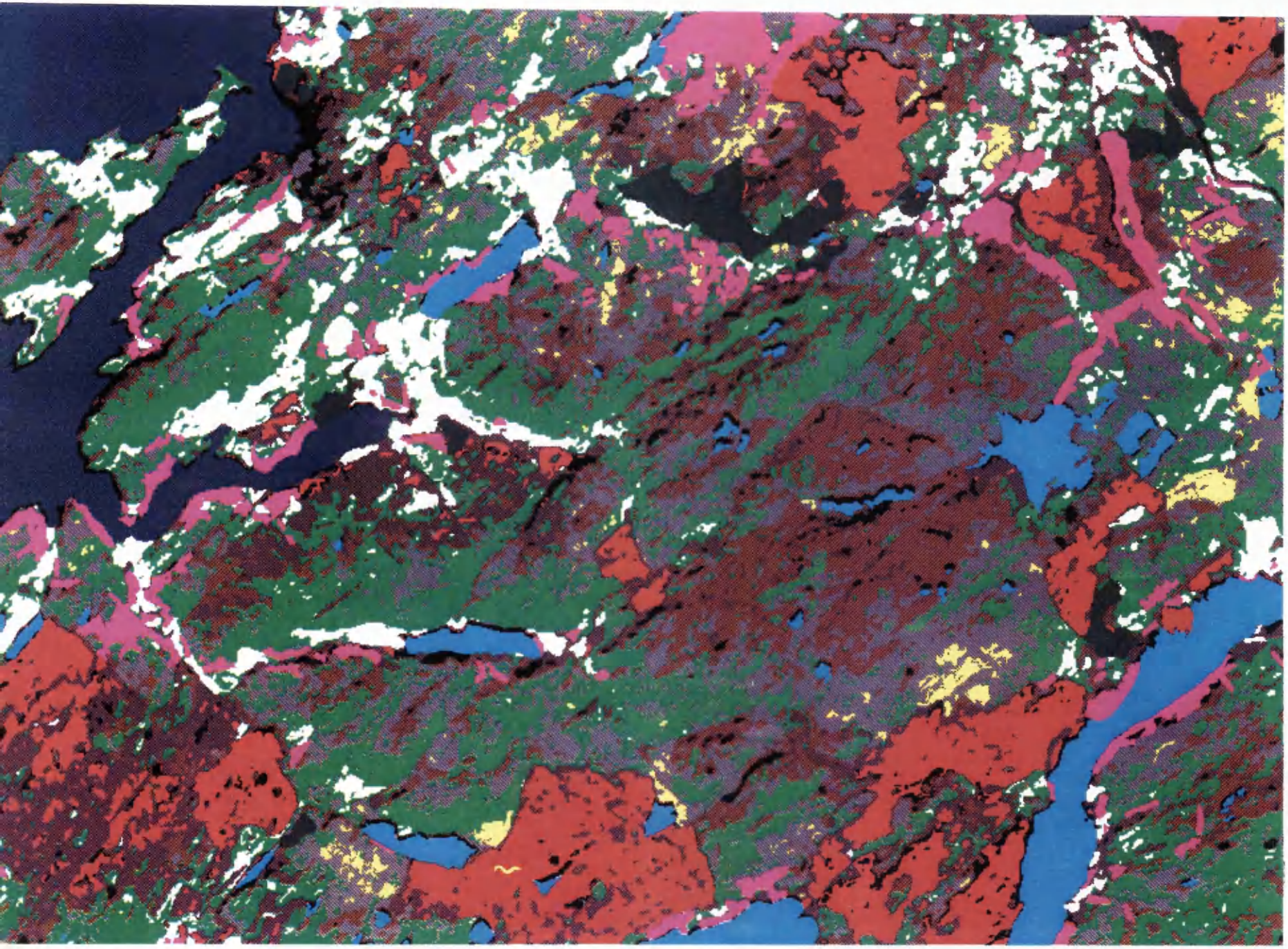
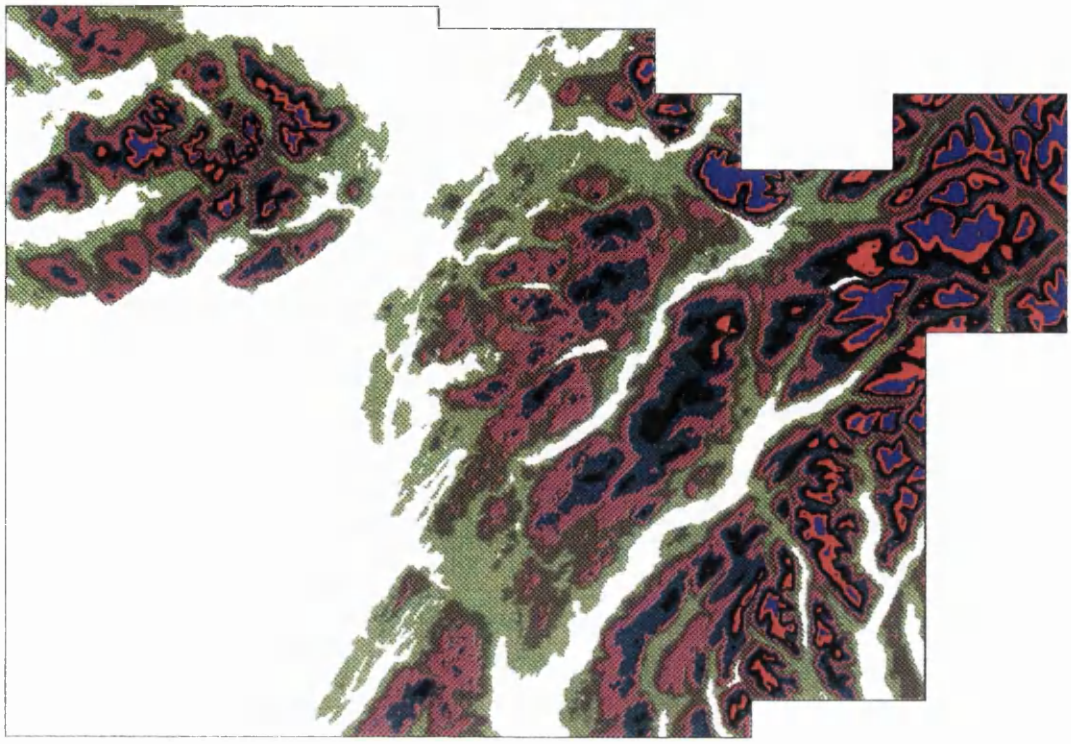


Figure 5.12 12 class land cover GIS layer derived from Landsat images. Enlargement of windowed area shown in Fig. 5.11 to show detail



Key

> 1m to ≤ 100m

> 100m to ≤ 200m

> 200m to ≤ 300m

> 300m to ≤ 400m

> 400m to ≤ 500m

> 500m to ≤ 600m

> 600m

Figure 5.13. Classified GIS layer of altitude after masking had removed areas of water.

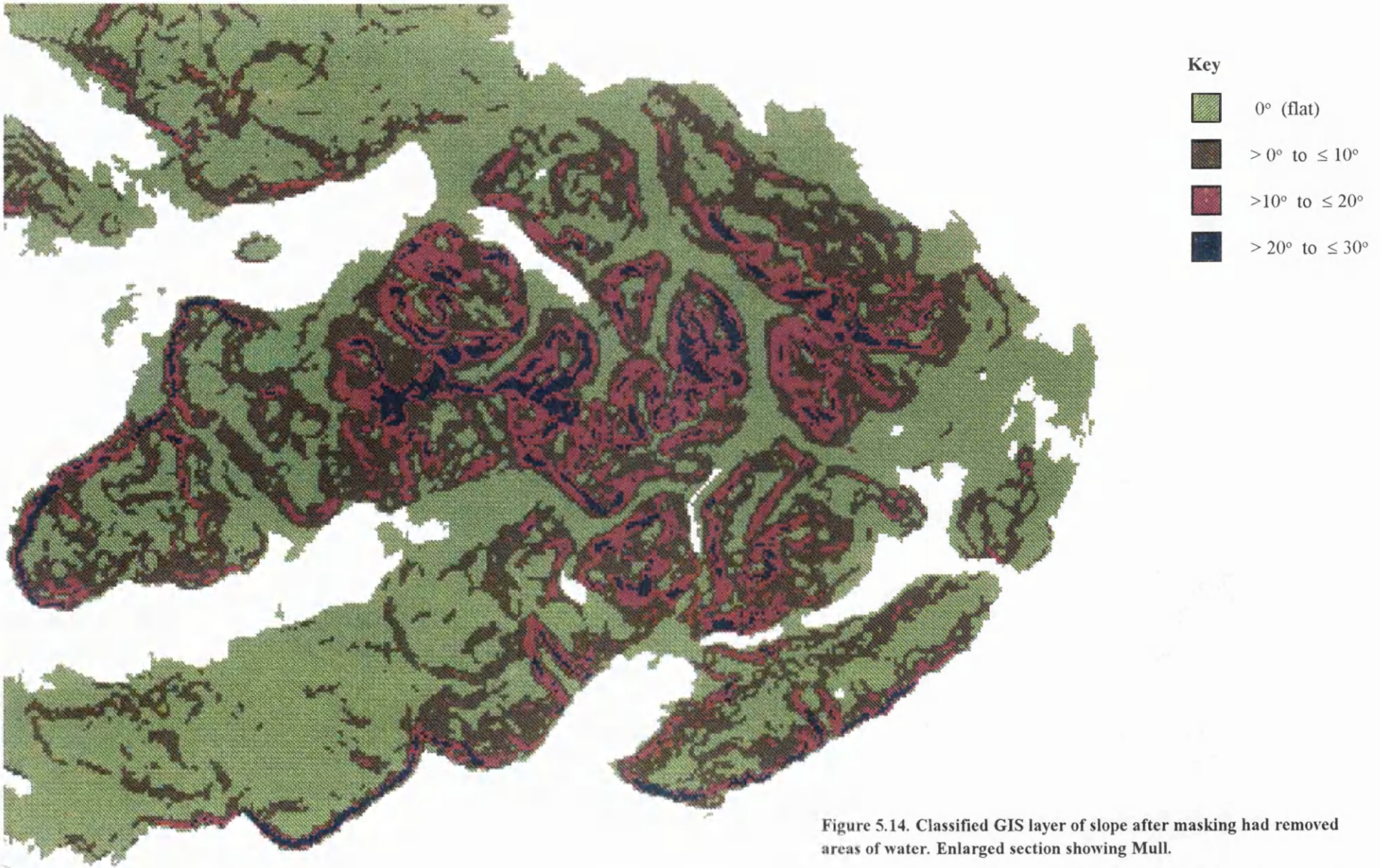


Figure 5.14. Classified GIS layer of slope after masking had removed areas of water. Enlarged section showing Mull.

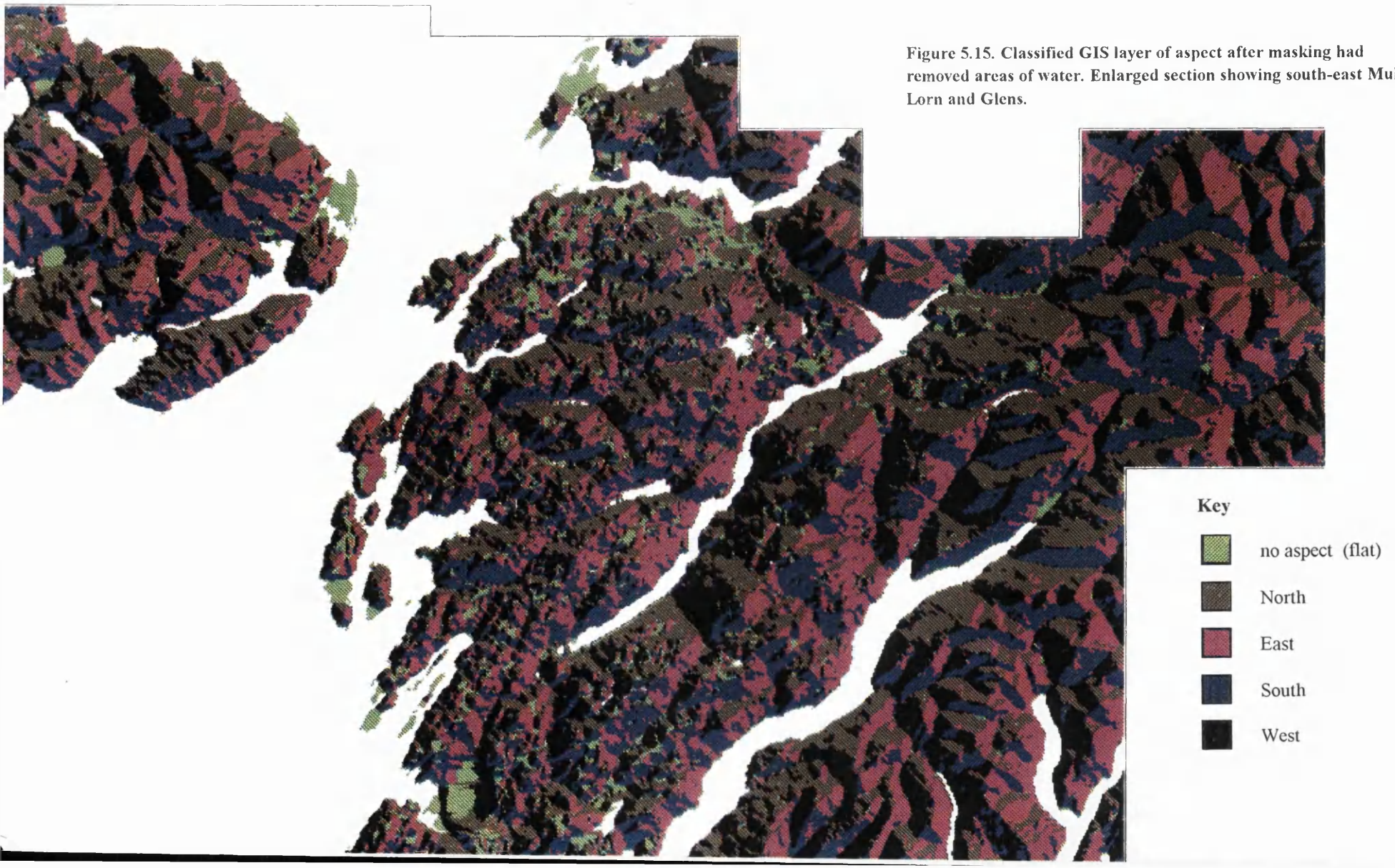


Figure 5.15. Classified GIS layer of aspect after masking had removed areas of water. Enlarged section showing south-east Mull, Lorn and Glens.

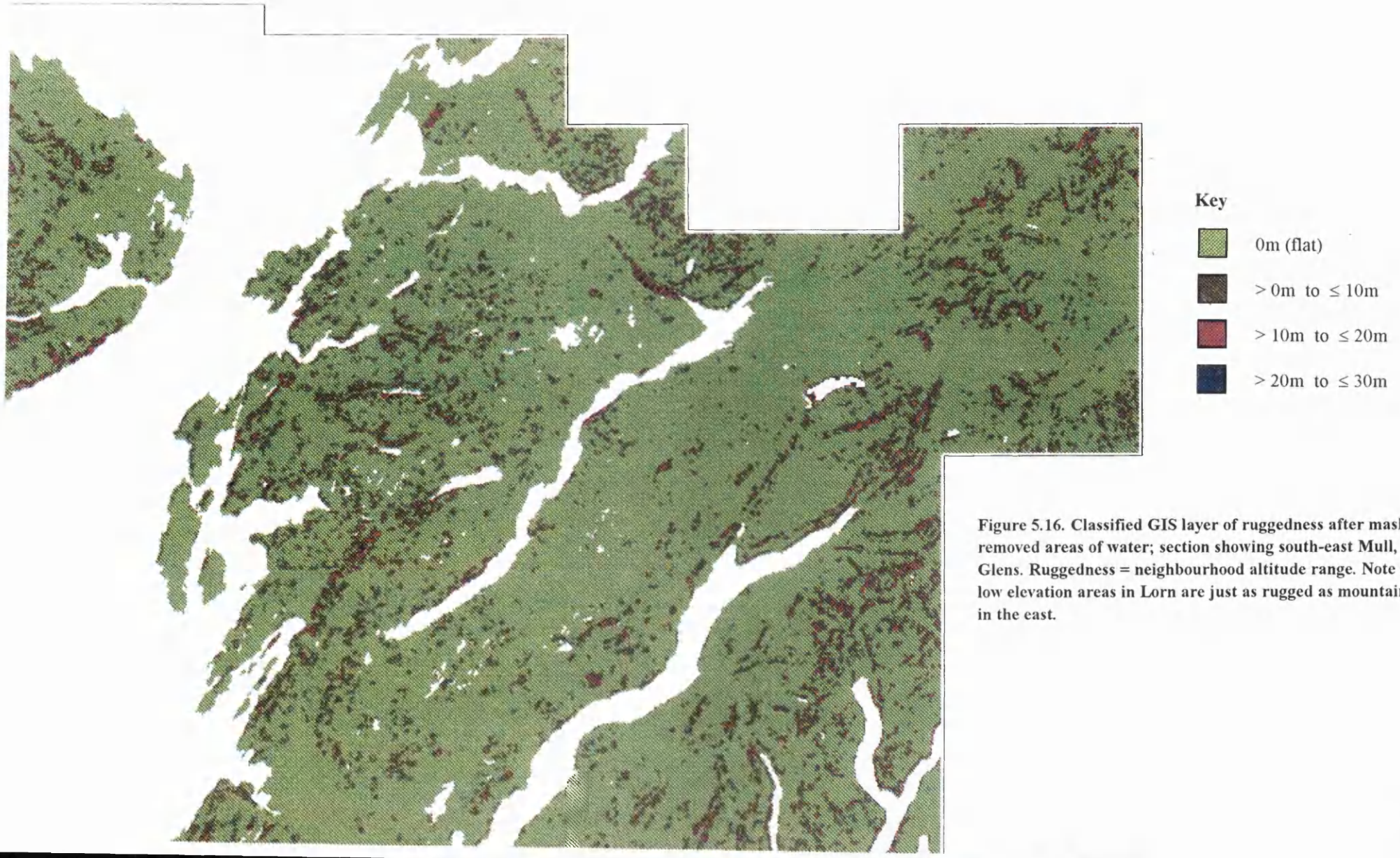


Figure 5.16. Classified GIS layer of ruggedness after masking had removed areas of water; section showing south-east Mull, Lorn and Glens. Ruggedness = neighbourhood altitude range. Note that some low elevation areas in Lorn are just as rugged as mountainous areas in the east.

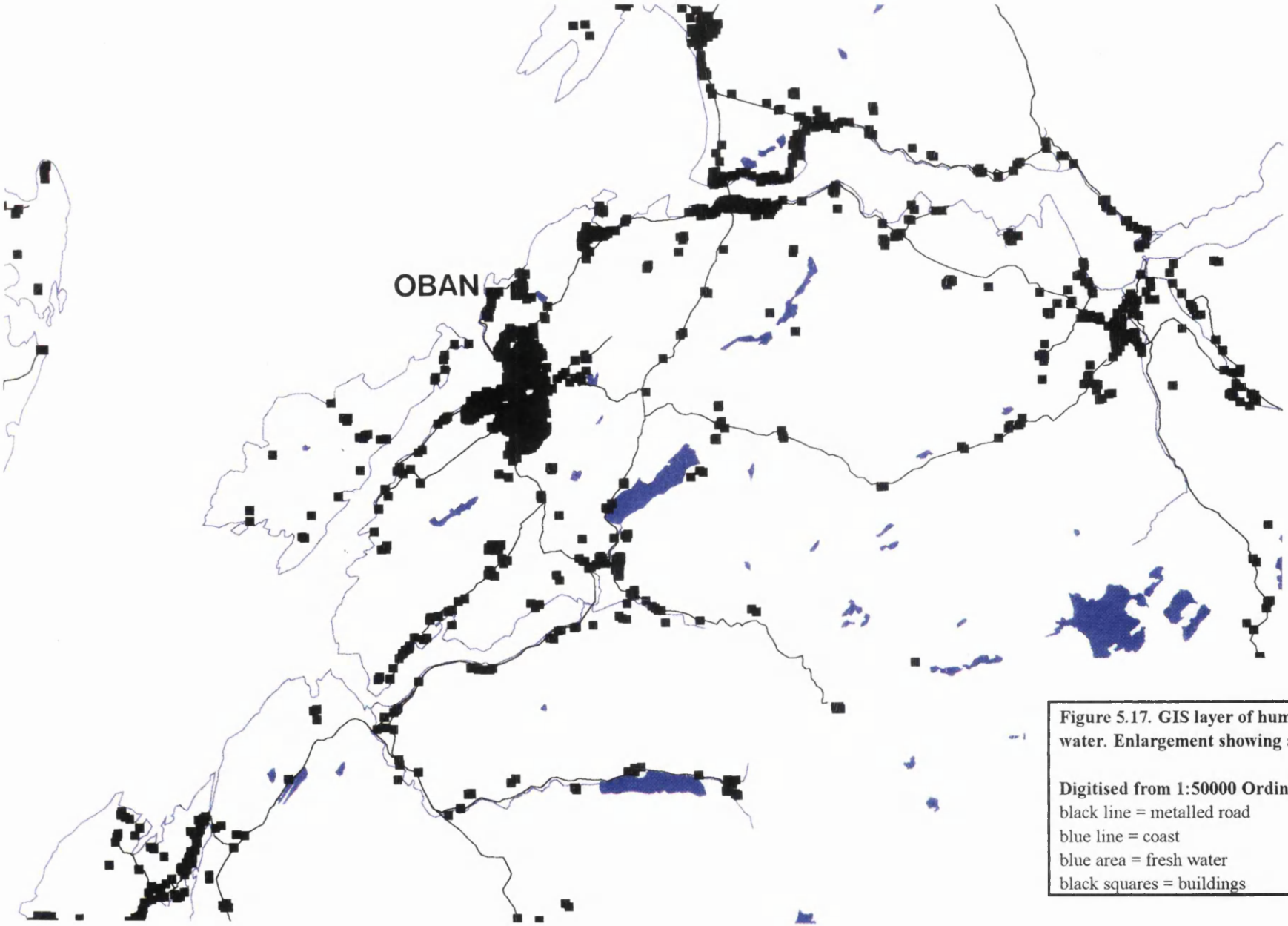


Figure 5.17. GIS layer of human culture overlaying water. Enlargement showing area around Oban.

Digitised from 1:50000 Ordinance Survey maps
black line = metalled road
blue line = coast
blue area = fresh water
black squares = buildings

PART II. DATA EXTRACTION

THE PROBLEM: CHOOSING AN APPROPRIATE SAMPLING UNIT

When modelling habitat suitability for an animal, the first decision that must be made concerns the size of the area over which habitat should be measured. When considering a region around, for example, a nest site, appropriate radii may be chosen in the absence of home range boundaries. When data are collected on a grid square basis, the size of the grid square must also be appropriate. Choice of sampling unit affects all subsequent modelling, yet has received very little attention in published work. Too large a unit, for example habitat within 1km squares related to presence/absence of species with territories considerably smaller than this such as dunlin *Calidris alpina*, lapwing *Vanellus vanellus*, and wheatear *Oenanthe oenanthe*, as used by Aspinall and Veitch (1990), obscures habitat effects at the level of the territory and results in very general habitat models. If the unit is too small, and perhaps only a small proportion of the home range, then the modelling will be related more to nest site selection than habitat suitable for occupancy. For example, Haworth and Fielding (1988) modelled presence or absence of breeding merlins *Falco columbarius*, which generally nest no closer than 2-3 km apart in Wales and rarely within 1km of each other elsewhere in Britain (Bibby, 1986). They sought to relate this to presence or absence of habitat features measured on a 0.25km grid. They found the presence of sloping ground with *Calluna* or *Pteridium* to be the best predictor of presence. This reflected the preferred nest sites of merlins in their study area rather than areas suitable for occupancy. The same general criticisms can be applied to Haworth and Thompson's (1990) analysis, although they and Thompson and Brown (1992) acknowledge this issue.

Thus data for modelling the influence of habitat on occupancy and breeding performance should be taken from an area approximating to home range size. When examining the separate influences of components of habitat, this represents no problem since data can be extracted from a suitable radius or grid centred on the nest or random locations. This commonly used approach does not, however, take into account the proximity of habitat components to the central point within the radius: two territories may contain the same amount of preferred

habitat, but in the one, it may be in one block surrounding the nest while in the other, it may be distributed around the periphery of the territory. In addition, for species such as the raven, there are no good data on which to base an estimate of home range size, except observed nearest neighbour distance, but even then home ranges may overlap.

If it is desired to use models to predict the suitability for all locations in a region, further problems arise. Since the infinite number of locations that are not nest-sites cannot all be considered, some method of grouping locations into a reasonable number of units must be undertaken. Regular grid squares are an obvious solution and that most commonly employed. However no one grid size can be adequate. If the cell size is large, approaching home range area or larger, then arbitrary grids may contain habitat not representative of the habitats within a radius around many potential locations within that cell. At the extreme, locations in the corner of grid cells have only one quarter of their surrounding habitat within the cell. Conversely, considering only the centre point of cells in an arbitrary grid at this size ignores many potential locations within the cell which may be centred in suitable habitat whereas the centre point may not. If cell size is too small, then the habitats it contains may not be representative of the habitats within the potential home range centred at locations within it. These considerations are further compounded by the scale at which the habitat is measured and the degree of heterogeneity in the landscape.

ONE SOLUTION: MULTIPLE SAMPLING UNITS AND A MINIMUM UNIT OF LOCATION

In this thesis, I have addressed these problems by sampling regions of increasing size around points. When choosing regions around a point of interest, an initial small area was measured, and then incrementally increased to beyond the likely home range size. In studies where home ranges are mapped, a similar procedure could be followed, as buffered zones within this can be measured separately. This approach produces a data set for inductive modelling which can take account of spatial distribution of habitat components within regions around points. In the case of ravens, where there were no good *priori* reasons for selecting a particular radius,

this also permitted separate examination of the influence of habitat on occupancy within a range of areas around the nest.

Similarly an incremental area approach was taken to produce habitat suitability maps for the entire region. The entire study area was divided into small (0.5km) grid cells. At this scale, the differences in habitat within a radius of likely home range size (3-5km) around any point within the cell were unlikely to vary to any great degree. Consequently habitats in areas around the central point in the cell were considered representative of the same areas around all potential points in the cell. Thus 0.5km Ordinance Survey squares (0.25 km^2) were chosen as the 'minimum unit of location'; that is, the finest resolution at which location was measured. In any study, the geometric basis for these minimum units of location will be a regular grid. **Since these locations are referred to often in the following chapters, I have given them the acronym GUL (singular) or GULs (plural), standing for 'Grid Unit of Location'.** As before, habitats were measured incrementally from small areas, well within the likely home range, to larger areas around each cell. The results of predictive modelling could be applied to each of these data to produce probability maps of the entire study area at a scale of 500m. Unlike previous grid cell mapping of habitat suitability, the resulting maps do not represent cells which contain suitable habitat, but grid cells which are at the centre of an area of suitable habitat. This seems a more biologically meaningful way of measuring and displaying habitat suitability, and one which overcomes the problems inherent in the traditional techniques described above.

As previously discussed, the extraction of habitat data around points from paper maps is extremely time consuming and error prone. This severely limited the amount, variety and quality of data which could be obtained with reasonable effort, and restricted ecologists to variations on the themes of the techniques criticised above. I was able to dramatically increase the quantity and quality of data extraction by use of the GIS. However, use of the GIS did not just permit a more efficient method of repeating past procedures but opened up previously unavailable opportunities to investigate the relationship of an animal and its environment. Indeed these opportunities are likely to lead to a range of solutions to problems such as those raised above.

METHODS

Defining a coverage of minimum units of location - GULs

A new coverage was made in Lites2 using **istart/os** with 500m Ordinance Survey grid lines. These were converted into 500m x 500m square polygons using **ilink/merge, ilink/break, ilink/structure** and **ipolygons/polygons** as described for the production of woodland polygons earlier. The central point in a polygon was computed during this procedure and each given a unique feature serial number. Polygon boundaries were deleted leaving a coverage of individually identifiable points regularly spaced at 500m intervals across the entire study area corresponding to the GULs. As the region around each GUL in which data would be extracted extended to 5km, a buffer of this distance was constructed within the GIS study area boundary and GULs within this deleted. The satellite derived vegetation raster map was overlaid with the coverage of the remaining GULs, and the value of each pixel within a 500m x 500m window around each GUL reported to a text file using **dti2text**. This was imported to Dbase4 for querying and production of a text file containing the identity of those GULs which contained only Landsat classes 12 or 13 (fresh and salt water). This was imported to the VAX where it was used by a macro to identify those GULs for deletion. Thus, those GULs which were centred in 500m polygons and which did not contain any land were removed from the coverage, since they could not possibly hold breeding ravens. There were 9677 GULs in the final GUL coverage (Figure 5.18).

Figure 5.18GUL coverage
Each cell represents 500m Ordinance Survey National grid squares containing land and within 5km of the study area boundary

Within the GIS the GULs were overlaid with the raven sites. Each GUL was assigned to an attribute class dependant on whether or not the GUL contained a raven site. GULs were also assigned to an attribute class dependant on which intensive study area they lay in.

Extraction of data for statistical modelling

Two types of data could be extracted from the GIS; vector and raster. Vector data could be extracted in regions of any shape around points of interest; by drawing in a surrounding polygon, cutting vectors at the junction with this polygon, defining the polygon as a region and querying the GIS for features contained within this region. Raster data could be queried in this way only by first vectorising the coverage using Laser-Scan modules to draw polygon boundaries enclosing homogenous blocks of pixels. This operation required a great deal of computing time, as regions were large and the raster maps very complex. Consequently this could not be performed for many locations and was restricted to regions around raven sites. Vector transformations of raster data not only permitted a count of total area in each raster class within the region but other variables

unavailable in raster format such as the patch size and length of patch boundary. Where data in regions around GULs across large areas were required, constraints in computing time forced me to work entirely in raster, unless vector data sets were simple, as in the case of raven sites, human habitation and roads. Extraction of raster coverage in regions was still a computationally demanding task and was most efficiently performed by obtaining counts of pixels in square windows around GULs .

Programming and macros

Each of these procedures required macros to conduct the repetition of actions at many sites. Since these macros were a repetition of the same actions at different locations, and consequently very long, 'master programs', written in a combination of Lamps, Lites2, Fortran77 and DEC control languages, were written to build the macros. Master programs were written to include interactive querying of the operator during program building, permitting choice of data sets to use, size of regions required, and format and destination of output. Seventy seven macros and master programs were written during the course of this study, many of which required several weeks of development and revision. None of this is reported in this thesis.

TIME TAKEN TO ESTABLISH THE GIS AND WRITE PROGRAMS FOR DATA EXTRACTION

Digitising of data and integration into the GIS took 4 months for two of us to complete: an estimated total of nearly 2,000 man hours. Image processing on the I.I.S. took an estimated 450 man hours, although this would have been substantially quicker had we not had to learn the system from scratch. Further classification in HORIZON took a further 200 man hours. Digital terrain modelling was achieved relatively quickly in two weeks. Working individually I estimate that it took 79 man-weeks just to establish the GIS.

Writing programs and macros was a substantially bigger task than anticipated, with an estimated development time of 36,00 man hours, or 90 working weeks for an individual with little prior knowledge of the system. Data extraction took me an additional five months. This was due to the size of the data sets, and the

requirement of running in low priority batch mode (therefore slower) because of the demands I was making on central computing facilities.

PART III ESTABLISHING THE ANALYSIS GIS

WHY USE A DIFFERENT SYSTEM ?

Statistical analysis had to be performed outside the Horizon GIS. As described above, the extracted data was transported from the VAX to a PC and converted into DBase4 relational database files prior to inclusion in statistical modelling. The results of this modelling were also placed in the DBase4 relational database, using the unique ID of each GUL to relate data and new attributes. Whilst these new attributes could have been translated and transported to the VAX, for convenience I used a PC based GIS system for mapping and presentation of results. This system also had the advantage of using Dbase format files: thus new attributes could be computed in SPSS PC+ and placed directly into the attribute tables of GULs in the GIS. Also, as will be seen in Chapter Eight, I required the use of a GIS to perform some statistical operations, and the use of systems which used the same data format greatly reduced the complexity of the task.

Equipment.

I used Environmental Research Systems Inc. PC Arc/Info version 3.4D (E.S.R.I., 1990) running on a Ti'Ko SB450 PC clone with 486DX processor (maths co-processor on board) running at 50Mhz, with 16Mb RAM, a 1Mb graphics accelerator card, and 245 Mb hard disk operating MSDOS 5. Arc/Info has very limited raster capacity and is effectively limited to vector data.

Making the GUL data base

Within Arc/Info, an empty coverage was defined using minimum and maximum coordinates of the environment GIS. A 500m Ordinance Survey grid was automatically added to this using the 'grid' procedure, and converted to 0.25km^2 polygons using 'clean' and 'build' polygon procedures. The absolute coordinates of GULs on land, along with their unique ID number, were converted from the Laser-Scan IFF format to the

Arc/Info text format, and an Arc/Info point coverage of these was created using procedure 'generate'. These were overlaid onto the 500m grid polygon coverage and used as seed points for new polygon labelling. Thus a coverage of 500m Ordinance Survey grid polygons was generated, with a polygon attribute table which could be accessed in Dbase4 and related by GUL ID numbers to data in the raven database and data from the environment GIS. New attributes for GULs (such as the presence or absence of nest site, logistic regression probability score etc.) were easily added to the polygon attribute file as new fields using simple Dbase programs.

COMMENT ON THE USE OF GIS FOR ECOLOGICAL RESEARCH PROJECTS

It is clear that setting up a GIS of this complexity for such a large area is a substantial task, especially if some of the layers must be obtained by extensive fieldwork as in this case. The obvious and attractive benefits of taking a GIS approach should be weighed soberly against the time taken to produce results. Long term (>5 years) ecological projects investigating spatial effects will most likely benefit from a GIS approach, but only if the requirements of the technology are accounted for at the outset. The availability of good equipment and, most importantly to a novice user, expert support in system management and the GIS are essential. However, the increasing power of personal computers, an increased flexibility and 'friendliness ' of GIS systems and wider availability of digital data, are likely to improve substantially the potential of this application for short-term ecological research projects.

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INTRODUCTION TO CHAPTERS SIX TO NINE.

When examining animal distribution two questions are commonly posed: 1) what makes habitat suitable or unsuitable?; and 2) where is the suitable habitat? In answering the first of these questions workers frequently turn to multivariate statistical analysis. This is felt to be an improvement on univariate approaches which are obviously incomplete when considering the complex interaction between an animal and its environment. However, ecological field data is prone to violate underlying assumptions required for most multivariate statistical analyses. Multivariate models can be used in two ways: descriptive (predictive) or inferential. In general, predictive modelling is more robust under conditions where assumptions are violated than using the same techniques for inferential purposes (Tabachnick and Fidell, 1989). In addition, predictive modelling has the added advantage that models are testable. Several authors have pointed out the dangers in adopting inferential multivariate techniques on ecological data which violate assumptions inherent in the tests (e.g. Williams, 1983; Rexstead *et al.*, 1988). Ecological inference from the results of such modelling should therefore be made with due caution.

Whilst the question of what makes habitat suitable or unsuitable is the one most commonly addressed by ecologists, conservation managers most frequently require the answer to the second question posed above: 'where is the suitable habitat?'. In addition they need to know what will happen to suitability if habitat is altered in order to predict the impact of land-use changes. These questions are best addressed by predictive models. Hobbs and Hanley (1990) emphasised the importance of prediction in habitat evaluation by correlating animal performance with habitat characteristics, particularly as this approach requires no understanding of the processes controlling population behaviour. Although such models are enhanced by an understanding of cause-and-effect relationships, this is extremely difficult to obtain for any animal. Ravens present particular difficulties for such a mechanistic approach given their breeding density, habitat and habits. In order to avoid this, and the statistical pitfalls outlined above, I adopted a purely predictive approach to answer the following questions: 1) how to predict suitable and unsuitable locations?; and 2) where were they? In determining the

latter I was also able to address another fundamental question concerning ravens in mid-Argyll: were all suitable locations filled, or were there gaps in the distribution which could not be explained by habitat, at least as measured in this study ? This is an important consideration for conservation managers. If apparently suitable gaps can be identified they can be targeted for more detailed investigation, and attention also turned to recruitment. The use of a GIS in this study provided a technique for modelling habitat change. This is discussed in Chapter 10 but not simulated, as predictions would be untestable in this short term study.

Each of the following chapters provides one step in a sequence of procedures designed to identify the most suitable locations for ravens. These use a combination of deductive modelling (that is using existing knowledge as a filter) and inductive modelling (inducing relationships from the data to act as a filter) to successively eliminate 500 grid units of location (GULs, as described in the previous chapter) within intensive study areas, where the distribution of all ravens were known. Where possible predictions were tested by split sample validation techniques. In addition final predictions were made for a large area in the centre of the study area and compared to the partial coverage of raven sites known in this area. Extensive use was made of the 'analysis' GIS to display the location of results at each stage. Although limited ecological inference was made from statistical analyses, it was hoped that the resulting maps would also aid interpretation.

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CHAPTER 6. DEFINING GAPS IN THE DISTRIBUTION OF RAVEN TERRITORIES USING NEAREST-NEIGHBOUR DISTANCES

INTRODUCTION

In Chapter 4 I described the tendency towards a regular distribution of raven nests found in mid-Argyll and elsewhere. However this does not imply an even distribution across the landscape, and examination of published distributions invariably show gaps. These gaps may be due to some aspect of the environment rendering the area unsuitable for ravens or failure of ravens to occupy a suitable location. In order to tackle the question of whether or not there were true gaps in the population it is, therefore, first necessary to eliminate apparent gaps where habitat or lack of nest sites prevent ravens from occupying land. In this chapter I produce distribution maps of all gaps in the study area. In subsequent chapters I go on to eliminate gaps which were due to lack of nest-sites or suitable habitat in the course of habitat suitability modelling.

In the absence of mapped territory boundaries, nearest neighbour distance (NND) from known sites offers a convenient method of locating gaps in a regular distribution, and is a common technique used by field surveyors to target searches for undiscovered sites. However the use of NND requires the assumption of a circular area of influence based on some point, usually taken from the nest. Clearly this area is unlikely to correspond exactly to home range in many cases, for instance pairs nesting along the coast. However, for birds such as ravens, which rarely engage in boundary disputes, dispersion appears to arise from mutual avoidance, or passive repulsion, up to a certain distance from the nest. Ratcliffe (1962) referred to as this distance as the 'proximity tolerance distance' and this is most likely to occur in even measure around each nest site. The mean NND in a population is therefore a measure of the average proximity tolerance distance between pairs in a locality. However, factors other than the proximity tolerance distance may affect mean NND within any locality. Some pairs' nearest neighbours may be further away than this distance due to patchiness of suitable habitat or nest site availability, and some neighbours in any year may be within the tolerance distance where a stable distribution has yet to be established (creating what Ratcliffe, 1962, called 'a local tension in the

population'). Ratcliffe (1962) also noted that a clumped and restricted distribution of suitable nest crags may result in local densities of a few pairs being unusually high for the region.

In this chapter I use mean NND as a measure of proximity tolerance distance, after removal of some extreme values, and determine the location of gaps in the distribution of ravens occupying territories in mid-Argyll in 1990.

METHODS

I searched for gaps which occurred in one year only, 1990, and within the four intensive study areas within the GIS study area. In this year and for these areas occupancy at all sites was known (see Chapter 2). 500m grid cells (GULs) were employed as the smallest unit of measurement of location as described in Chapter 5. A map of GULs within intensive study areas and the distribution of GULs occupied in 1990 is given in Figure 6.1.

Raven to raven nearest neighbour distance

Mean NND figures for each intensive study area were calculated in Chapter 4 .

GUL to nearest raven distance

The map of all GULs on land within the four intensive study areas LORN, MULL, GLENS and COWAL was overlaid with the map of all known raven sites in the Lites2 mapping package (the mapping package for the Laser-Scan Horizon GIS, see Chapter 5). A Lites2 macro was written to search for every GUL and at each find every raven site within a 5km radius around the centre of the cell. For each GUL a record was made of 1) the unique identity of the GUL; 2) the identity of each raven site within the radius; and 3) the difference between the x and y coordinates of the raven and GUL locations in metres. This data set was transferred from the VAX to a PC and translated into DBase4. The distance between each GUL and its surrounding raven sites was calculated in Dbase4 by Pythagorous' theorem. A Dbase4 program was written to calculate the distance from each GUL to every raven site occupied in 1990 within 5Km of the GUL, and then select the smallest to give

the distance to the nearest raven site. These data were coded into Arc/Info GUL polygon attribute tables for querying and mapping.

Analysis

All statistical procedures were done using SPSS PC+ v4.01 (Norušis, 1990). I used the terms 'vacant' and 'not vacant' when referring to the potential of a GUL to hold a new pair of ravens to avoid confusion with the terms 'occupied' and 'unoccupied', which I have used throughout this thesis to refer to the status of known raven sites.

The mean NND for the four intensive study areas within the coverage limits of the environment GIS (i.e. excluding Tiree) were compared using a one-way ANOVA. As all sites were known, rather than a sample, pairs of sites which were each others nearest neighbour were treated as independent. GULs which were located less than the mean NND for that area from a raven site were considered 'not vacant', that is unable to be occupied by a new pair of ravens because of the influence of a nearby existing pair. Consequently, GULs containing such sites unoccupied in 1990 were classified as 'vacant' or 'not vacant' depending upon NND criterion. I examined group statistics to determine if the use of separate intensive study area means was justified.

RESULTS

Distribution of gaps

Summary statistics for raven to raven NND for sites occupied in 1990 in the intensive study areas are presented in Table 6.1. There were significant differences between the mean NND of intensive study areas (one-way ANOVA, $F_{3,47} = 3.28$, $p = 0.029$). However, a Tukey multiple comparisons test indicated the only significant difference was between Mull and Cowal.

Using the mean NND for each region to classify GUL's, there was a great difference in the amount of ground apparently vacant in each intensive study area (Table 6.2). MULL had the lowest proportion of vacant GULs followed by COWAL, LORN and GLENS respectively. Most of these GULs were aggregated in a few large, discrete blocks (Figure 6.2). However, it is important to note that these estimates are based upon figures which may have been distorted by variation in patchiness of habitat between areas. The mean NND for MULL and GLENS was large because of values which were likely to be a result of a patchy distribution of ravens rather than mutual avoidance. At a mean NND of 5Km the expected population density based on the regression from observed values given in Figure 4.3 was estimated to be 0.95 pairs/100km^2. It is unlikely that any manifestation of territoriality could occur at such a density. When only sites with a NND of less than 5km were considered, the mean NND for MULL was 3.3Km (s.d. = 1.0, n = 11) and GLENS was 3.7 (s.d. = 0.9, n=3). Conversely the mean NND for COWAL was small because of two sites which were only 1.7km apart. Although these two sites could not be removed on statistical grounds, their proximity was unusual for the area and territorial disputes appeared unusually common. One of the sites had not been present in 1989, and the fact that both pairs failed in 1990 increased my suspicion that this distribution of nest sites was unstable. When these two sites were excluded the mean NND for COWAL was 3.3km (s.d. = 0.6, n = 5). With these sites excluded from MULL and COWAL the new overall mean NND was 3.4km (n=43, sd=0.7) and there was no significant difference in the mean NND between groups (one-way ANOVA, $F_{3,39} = 0.40$, p=0.77). The overall mean NND was consequently used to reclassify all GULs as vacant or not vacant in all intensive study areas (Figure 6.3 and Table 6.3).

area	mean NND (km)	min NND (km)	max NND (km)	n	s.d.
overall	3.6	1.7	6.4	51	1.1
COWAL	2.8	1.7	4.2	7	0.9
GLENS	4.2	3.2	5.5	4	0.9
LORN	3.4	2.4	4.6	24	0.5
MULL	4.1	2.4	6.4	16	1.5

Table 6.1 Summary statistics for nearest neighbour distance (NND) of raven sites occupied in 1990 by intensive study area.
As the complete distribution of pairs in each area was known each site's NND was considered independent.

area	GULs vacant	total GULs in area	% vacant
COWAL	126	543	23
GLENS	339	662	51
LORN	986	2746	36
MULL	150	1579	9

Table 6.2 Number of 500m grid cells (GULs) classed as vacant in each intensive study area in 1990 using individual area mean nearest neighbour distances (NND).
GULs lying closer than the mean NND for that area to a raven site occupied in 1990 were considered 'not vacant'.

Using the overall mean NND to classify GULs increased the number of vacant GULs on MULL and decreased them in COWAL, with little difference to GLENS or LORN. The distribution of vacant GULs remained confined mainly to a few aggregations, with most vacant ground in the east of LORN and GLENS. I estimated the maximum number of raven territories that could have been fit into areas classed as vacant by fitting as

many solid disks of radius 0.5 x overall mean NND (1.7km, at the same scale as maps) into these areas (Table 6.4).

area	GULs vacant	total GULs in area	% vacant
COWAL	56	543	10
GLENS	391	662	59
LORN	985	2746	36
MULL	360	1579	23

Table 6.3 Number of 500m grid cells (GULs) classed as vacant in each intensive study area in 1990 using overall mean nearest neighbour distance (NND).
GULs lying closer than 3.36km to a raven site occupied in 1990 were considered 'not vacant'.

area	number of occupied territories in 1990 [1]	number of unoccupied territories in 1990 [1]	number of hypothetical 'missing' territories [2]	% missing [3]
COWAL	7	4	5	42
GLENS	2	0	17	89
LORN	26	6	44	63
MULL	17	4	23	58

Table 6.4 Number of hypothetical raven territories which could have been fit into vacant GULs
[1] in intensive study areas within GIS area. Unoccupied = previously occupied but now deserted.
[2] maximum number of non-overlapping circles of 1.7km radius (0.5 x overall mean NND) which could be placed in GULs classed as 'vacant'.
[3] (missing / [missing + occupied]) x 100

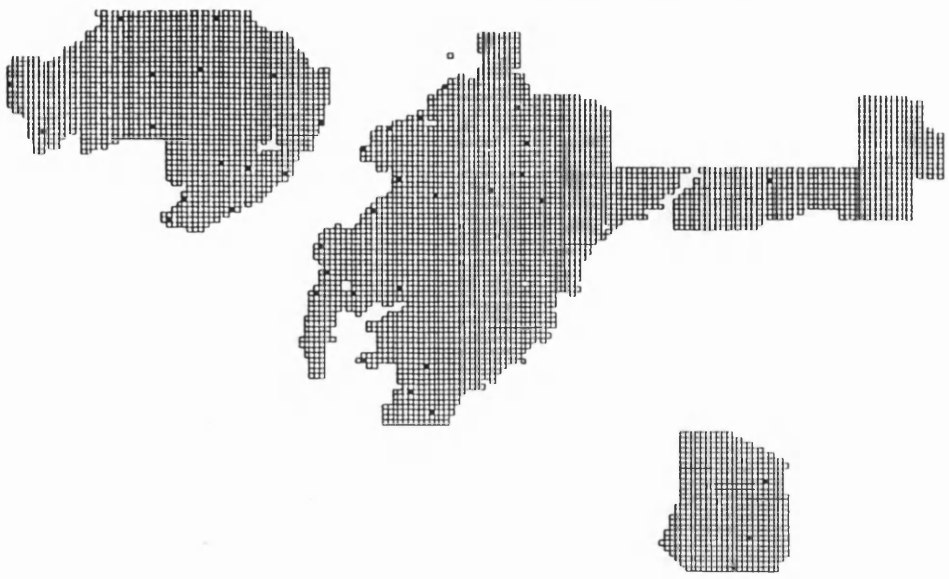

Figure 6.1 Raven occupancy of 500m grid cells (GULs) containing land and within intensive study areas in 1990.
■ = GULs which contained an occupied raven site in 1990.
□ = GULs which did not contained an occupied raven site in 1990.

Figure 6.2 500m grid cells (GULs) classed as vacant in each intensive study area in 1990 using individual area mean nearest neighbour distances (NND).
GULs lying closer than the mean NND for that area (see Table 6.2) to a raven site occupied in 1990 were considered not vacant (□); all others were classed as vacant GULs (■).

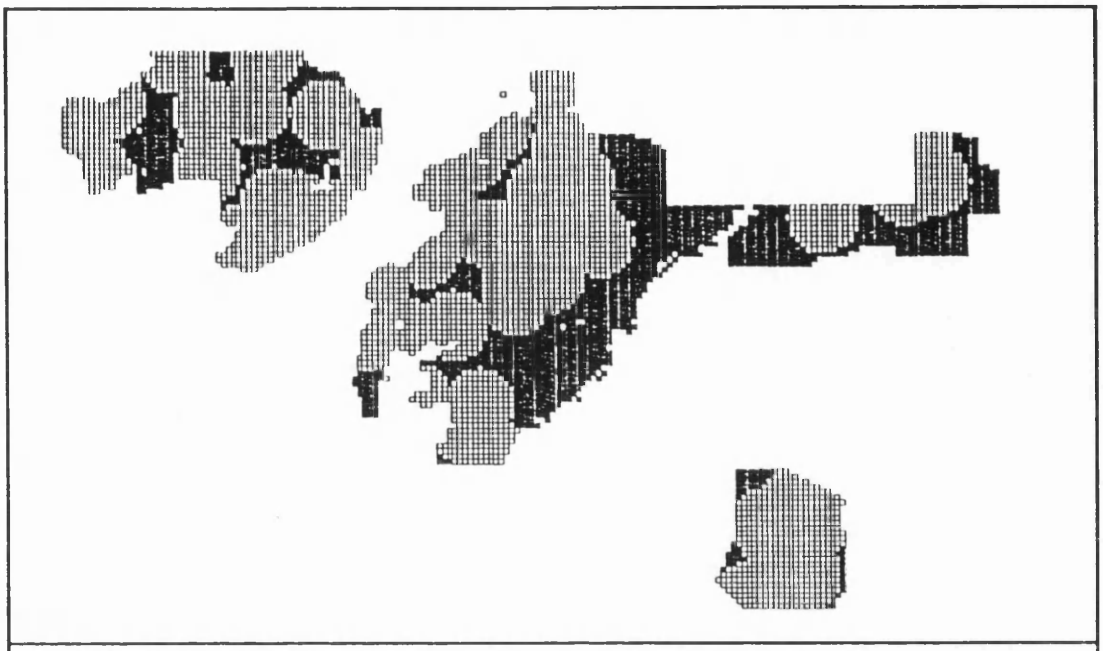

Figure 6.3 500m grid cells (GULs) classed as vacant in each intensive study area in 1990 using overall mean nearest neighbour distance (NND).
GULs lying closer than 3.36km (see Table 6.3) to a raven site occupied in 1990 were considered not vacant (□); all others were classed as vacant GULs (■).

DISCUSSION

There were many gaps in the distribution of occupied GULs in 1990. GULs classed as vacant tended to occur in large aggregations. This indicated that gaps were real and not artefacts of the methodology. Using a mean NND for the entire study area rather than mean for each intensive study area calculated separately changed the percentage of GUL's classified as vacant. However the change was small (+10.6%) and the distribution of aggregations was not changed. I consider the mean NND for the entire study area to be the best unit to use, considering the inherent assumptions in using NND, and unknown variance in this measure due to patchiness of habitat (see Newton, 1979, page 60).

Many studies of raptors with traditional territories have noted the tendency for some sites to be occupied irregularly (reviewed in Newton, 1979). As I used data from one year only I may have underestimated the true number of territories present over a number of years. Dare (1986), taking four consecutive years, found

average occupancy rates of 91% and 92% in two regions of north Wales (n = 290). Ratcliffe (1962) calculated an average occupancy of 94% over 12 years in four upland areas combined (n = 276). Davis and Davis (1986) reported occupancy to range between 88-100% over six years (n = 364). Based on the two years of this study I had an occupancy rate of 79% in mid-Argyll in 1990. This figure is probably artificially low as some historic territories included as 'unoccupied' may have been deserted for some time and would never be reoccupied. This was similar to the occupancy rates of 80-87% found by Davis and Davis (1986) when permanently deserted territories were included in their calculation. It was unlikely that unknown territories existed in intensive study areas in mid-Argyll as they were searched thoroughly, especially in apparent gaps (chapter 4).

Thus some locations classed as vacant may have proved to be irregular raven sites over the long term. As it tends to be only certain territories which are irregularly occupied, these presumably are of poorer quality than regularly occupied sites (Newton, 1979). However, the number of territories observed, even including all deserted sites, clearly fell short of the maximum number of hypothetical territories which the area could have held, and there were evidently substantial gaps in the distribution.

Locations may have been vacant for many reasons. In the next chapter I assessed the importance of nest site quality to ravens and determined if locations were vacant because of lack of nest-sites.

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CHAPTER 7. THE INFLUENCE OF NEST SITE QUALITY ON OCCUPANCY AND BREEDING PERFORMANCE OF RAVENS

In this chapter I establish if nest-site quality influenced breeding performance of ravens in mid-Argyll, and define the minimum requirements for a site to be suitable for occupancy. I then use the GIS systems to examine the distribution of vacant locations determined in Chapter 6 with the distribution of potential nest sites.

INTRODUCTION.

Nest-site quality may be an important determinant of breeding performance in birds, in terms of the degree of protection from the elements, predators and disturbance that the site affords, and in some species attractiveness to potential mates. The availability of suitable nest-sites can limit the size and distribution of a breeding population. This is most notably demonstrated when new pairs occupy artificial nest-sites provided in an area apparently short of natural sites, for example Pied Flycatchers, *Ficedula hypoleuca* (Lundsburg and Alatalo, 1991), and Ospreys, *Pandion haliaetus* (Poole, 1989).

Ravens and many raptors have very traditional nest sites. The birds usually select a site each year from a small number of alternative nest-sites in the territory. These sites are obviously favoured for some physical feature or combination of features, judging from the fact that when sites are reoccupied after an absence of many years the new occupants often choose to nest in exactly the same spot as the historic nest or eyrie (Ratcliffe, 1962). Cullen and Jennings (1986) report photographic evidence of exactly the same ledge being used in 1893 and the present day at a site on the Isle of Man. Nest-site requirements in raptors may be both for a certain kind of physical structure, for instance by choosing specific types or size of tree (Tjernberg, 1983; Speiser and Bosakowski, 1987; Loman, 1979), in addition to a suitable environment around the site such as proximity to food resources or human disturbance (Andrew and Mosher, 1982; Rich, 1986). Nest-site requirements of a species may vary in response to different environmental pressures. Mosher and White (1976) found that the

directional exposure of golden eagle (*Aquila chrysaetos*) nests varied in four regions of North America. They hypothesised that the preferred aspect of golden eagle nests was dependent on temperatures during the breeding season, these being mediated by latitude and elevation.

Ravens appear to prefer nesting on tall cliffs to smaller cliffs and trees (Ratcliffe, 1962). In population increases in some parts of Britain, this centuary, there has been a return to tree nesting as available cliffs ran out (Hollyoak and Ratcliffe, 1968). In some regions the lack of suitable nest-sites may influence population density, and on a local scale the distribution of pairs may be influenced by the distribution of preferred sites.

It may be reasoned that the relative merits of different sites might not be constant, perhaps only being decisive in years of particularly bad weather or high predator levels. During 1989 and 1990 there was no evidence of interference at nests by humans or predators (Chapter 2), but in any case this is probably constant from one year to the next. Only data for the year 1990 are presented: the spring of that year was one of the coldest and wettest for a decade, and a year in which any benefits of a well sheltered site would be manifest.

In Part I of this chapter, I establish if the physical characteristics of the nest site influenced site occupancy and breeding performance. On the basis of these findings the minimum criterion for a location to hold a raven's nest are determined. In Part II, I develop a method to determine which locations in the study area could be excluded from consideration as a potential raven site because they were extremely unlikely to contain a nest site.

PART I. THE INFLUENCE OF NEST SITE CHARACTERISTICS ON TERRITORY OCCUPANCY, BREEDING, BREEDING SUCCESS AND NUMBER OF YOUNG FLEDGED.

METHODS.

For clarity, I have used the conventions of Ratcliffe (1962) and Newton (1979), with additions, in describing nesting areas: "breeding site" is the physical location chosen for nesting; for cliff sites "nest-cliff" is used to describe the rock-face or range of crags used for breeding; "nest-site" refers to the precise location of the nest on the rock, tree or building; and "nest" for the structure built by the birds. "Nesting territory" refers to the area around the breeding site which is aggressively defended during the breeding season. In the case of ravens this area is much smaller than the "home-range" used for foraging. In this analysis I considered only data from 1990 as most sites were re-used in successive years and were not independent observations.

Nest site descriptions.

Descriptions were taken of nests in use in 1990 unless the territory was deserted or breeding not attempted, in which case information was collected for the most intact (i.e. probably most recently used) nest found. Information collected fell into three broad categories which I thought might influence nest site selection: shelter; protection from predators, especially man; and position in the landscape. As almost all nests in the study area were sited on cliffs, most measurements relate to cliff-sites only. Measurements were made on two scales. Nest-cliff parameters measure features pertaining to the cliff, that influence the suitability of that cliff for ravens. Nest-site parameters measure features in the immediate vicinity of the nest, that may influence the choice of actual nest location on a cliff. Shelter from the elements was thought to be particularly important in this regard and detailed measurements of the micro-topography of each site were taken. Descriptions were taken in the field for 65 nests used in 1990, using standard recording sheets. Breeding site altitude was later extracted from the environment GIS. Details of parameters measured are given below, along with an explanations for the inclusion of certain variables :

A) ALL SITES

1) **Type of site**: open cliff, cliff in gully, or tree.

2) **Nest Height**: height to nest (nearest metre, estimated by eye with reference to a mark at known height).

3) **Altitude of the nest-location**: obtained from the GIS by overlaying the map of raven nest sites with the unclassified raster map of altitude using a macro to report the pixel value at each nest (nearest metre).

B) CLIFF SITES ONLY

i) Measurements of the nest cliff

1) **Cliff height**: height of cliff at nest (nearest metre, except on very tall cliffs where precision of the estimate was in the region of nearest 5metres).

2) **Cliff aspect**: aspect to the nearest eighth cardinal point of the main cliff orientation.

3) **Number of ledges**: categories of the number of distinct ledges on the cliff apart from the one occupied by the nest (category 1=0, 2=1-4, 3=5-9, 4=>9). This was an index of cliff-face ruggedness. Cliffs with a greater choice of ledges may have been preferred.

4) **Cliff-face vegetation**: (0=none, 1=sparse moss/grass, 2=heavily vegetated, including dwarf shrubs, bushes and trees). Vegetation may provide shelter and camouflage.

5) **Cliff-face wetness**: (1=dripping water, 2=damp but no running water, 3=dry).

6) **Open view from nest**: (1=open view, 2=view obscured by trees etc.).

7) **Scree type below cliff**: (0=none, 1=some scree but localised and old, 2=substantial scree but mainly old, 4=substantial amount of fresh rockfall). Old rockfall was distinguished by overgrowth of vegetation and accumulation of soil. This parameter was an index of the friability of the cliff-face, which may influence stability of the nest platform and potential rock-fall into the nest.

ii) Measurements of the nest-site

1) **Nest aspect**: aspect to the nearest eighth cardinal point of the face immediately behind nest. The aspect of nests situated in a corner was determined as that of the vector given by half the angle between the two faces.

2) **Ledge length**: estimated by eye to the nearest 1m. Nests were sometimes positioned on a small outcrop or indentation in the cliff-face rather than well formed ledges and were recorded as having a ledge length of 0. Bigger ledges may have afforded a more substantial base for the nest, and a platform for pre-fledged chicks.

3) **Ledge depth**: as for ledge length but estimated to the nearest 0.5m.

4) **Nest under overhang**: (1=yes, 0=no). Nests were deemed to be overhung not only if they were under a definite 'roof' but also if sited on a outward sloping face.

5) **Height to roof**: for nests which were overhung, the distance between the outer rim of the nest and the overhanging rock, estimated by eye to the nearest 0.5m.

6) **Nest vegetation**: vegetation immediately surrounding the nest (classes as for cliff vegetation).

Analysis

All statistical procedures were done using SPSS PC+ v4.01 (Norušis, 1990). Statistical comparisons of nest-type, nest-cliff and nest-site variables were made between groups of territories, defined by a number of criteria. Territories were categorised into two occupancy groups defined by whether or not they were occupied in 1990; into two breeding groups defined by whether or not breeding was attempted in occupied territories; into two success groups defined by whether or not breeding attempts resulted in at least one chick successfully fledged; and into four fledging success groups defined by the number of chicks fledged from successful breeding attempts. For continuous variables, group medians were compared using Mann-Whitney U tests or Kruskal-Wallis one-way analysis of variance as appropriate. For binary variables, group differences were tested for significance using Fishers exact test. The null hypothesis was that there was no difference between groups, with an independent null hypothesis for each test. Rejection of null hypotheses by statistical tests was accepted at the $p<0.05$ level, with two-tailed probabilities. Each interval or ratio scale nest site description variable was checked for normality using a one sample Kolmogorov-Smirnov test, and examination of normal probability and detrended normal probability plots. Only the number of young successfully fledged had a normal distribution and so non-parametric tests were used throughout, with probabilities corrected for ties. Nominal data were converted into series of binary dummy variables for tests between territory groups. This analysis inevitably resulted in multiple univariate tests, as multi-way tests were not able to deal with the small cases to variables ratio, and it was accepted that 5% of results were likely to be due to chance alone.

RESULTS

Descriptions were made of nests in 65 territories, of which 49 were in intensive study areas (LORN 21; COWAL 6; GLENS 4; MULL 18).

Territory groups and fledged brood size.

At the 65 sites where nest measurements were made, 55 were occupied, 8 were deserted, and two were of uncertain status. Of the 55 which were occupied, 47 made a breeding attempt and of these 31 were successful in raising at least one young. The number of young fledged was known at 27 sites in the main study area: the median number of chicks fledged per successful pair was three. The two sites where occupancy was uncertain were also conservatively classed as non-breeding, and thus sample sizes of breeding plus non-breeding exceeds the number of occupied territories by two.

The independent influence of breeding site characteristics on occupancy, breeding, success, and fledged brood size.

Measurements of the continuous variables cliff and nest height, ledge depth and width and height to overhang are summarised in Table 7.1. Statistical comparisons of theses parameters between territory groups and with fledged brood size are presented in Tables 7.2a-d. The distributions of ordinal and categorical variables are shown in Figures 7.1a to 7.1i. Statistical comparison of these variables between territory groups and with fledged brood size (collapsed into three classes) are presented in Tables 7.3a-c.

Variable (m)	n	min	max	median
cliff height	65	4	99	17
nest height	65	2	70	9
ledge length	65	0.0	0.0	0.5
ledge depth	65	0.0	3.0	1.0
height to roof[1]	30	0.3	3.0	1.0
altitude[2]	49	0	558	127

Table 7.1. Summary of breeding site variables measured on a continuous scale for a sample of ravens breeding in Mid Argyll in 1990.

1 where under overhang

2. from GIS coverage of altitude. Only 49 of total of 65 sites were within the limits of this coverage

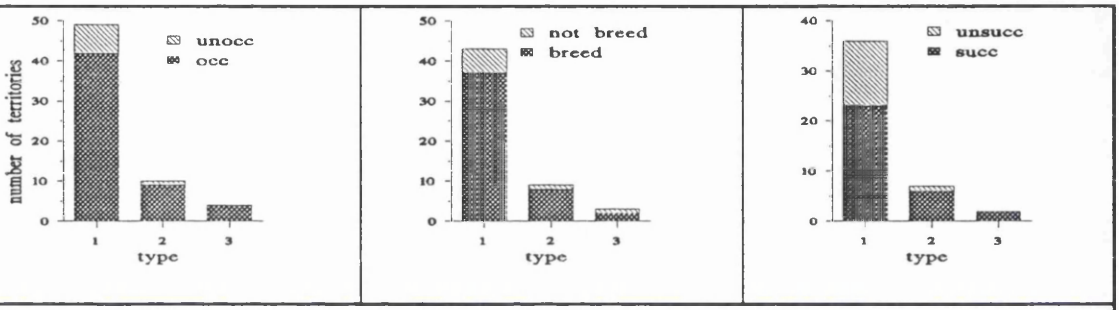

Figure 7.1a. Number of territories by occupancy, breeding, and success by nest-site type.

type 1= open cliff; type 2 = cliff in gully, type 3= tree.

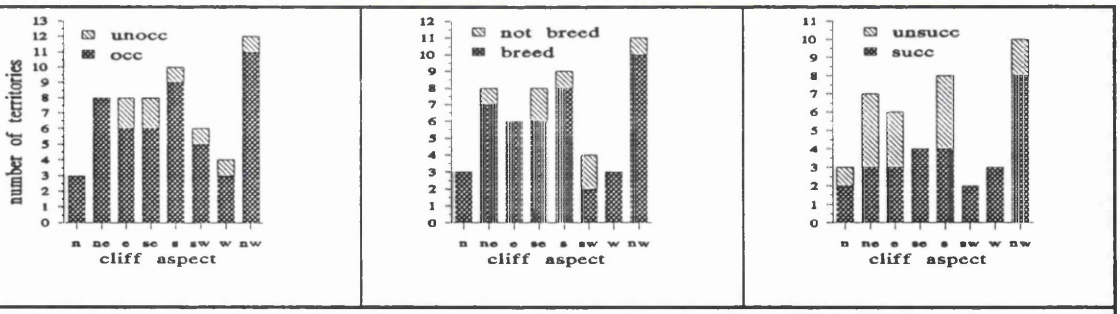

Figure 7.1b. Number of territories by occupancy, breeding, and success by cliff-face aspect.

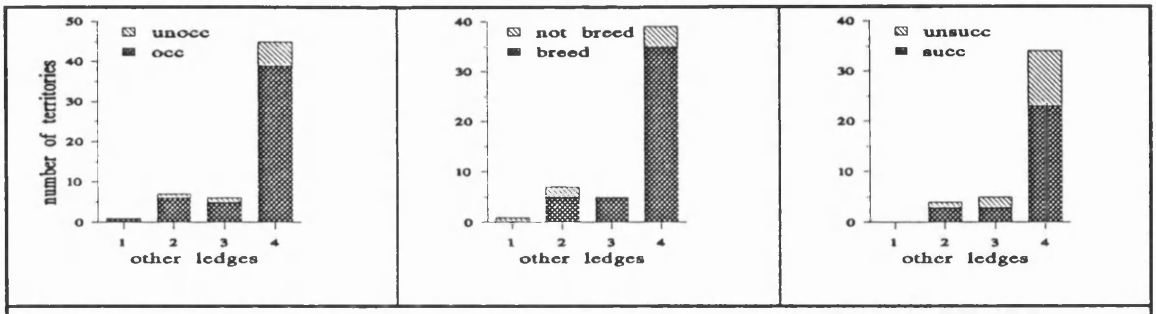

Figure 7.1c. Number of territories by occupancy, breeding, and success by category of other ledges.
ledge 1 = none, 2 = 1-4, 3 = 5-9, 4 = >9.

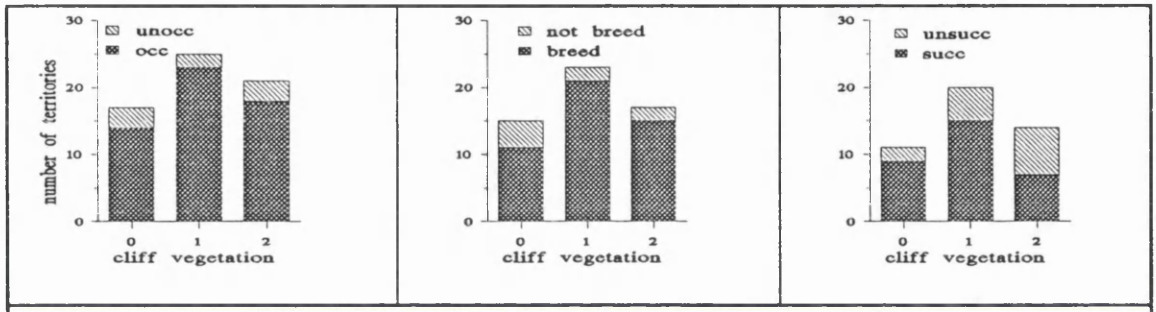

Figure 7.1d. Number of territories by occupancy, breeding, and success by cliff-face vegetation category.
vegetation 0 = none, 1 = sparse, 2 = heavily vegetated

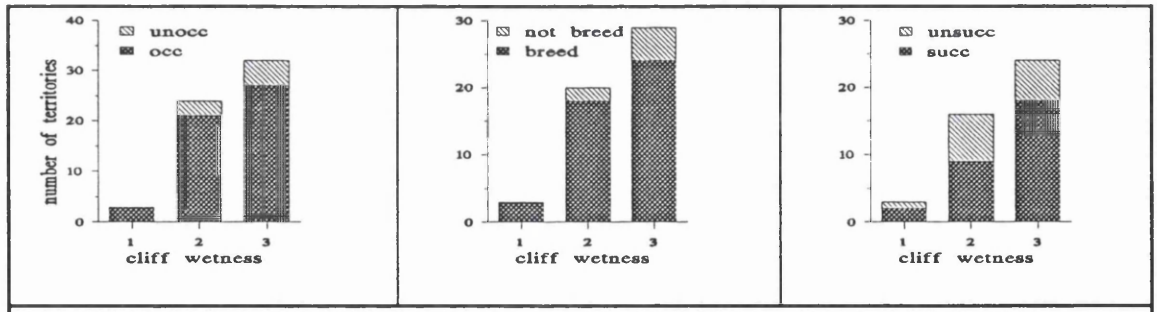

Figure 7.1e. Number of territories by occupancy, breeding, and success by cliff-face wetness category.
wetness 1 = dripping water, 2 = damp but no running water, 3 = dry.

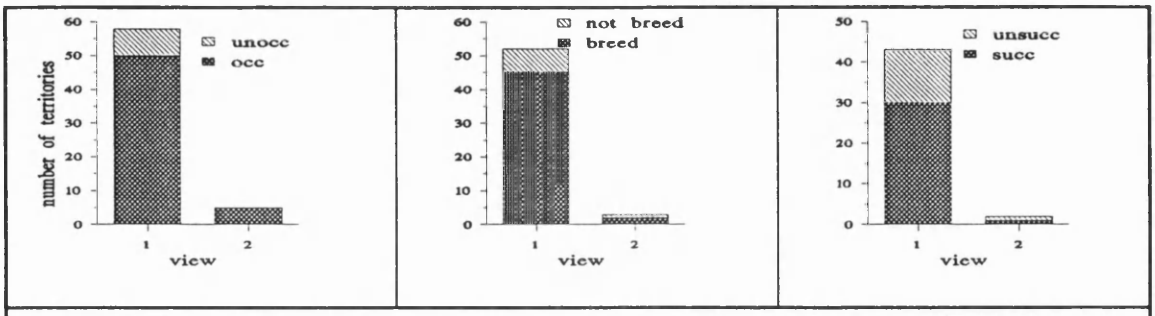

Figure 7.1f. Number of territories by occupancy, breeding, and success by class of view from nest.
view 1 = open, 2 = obscured.

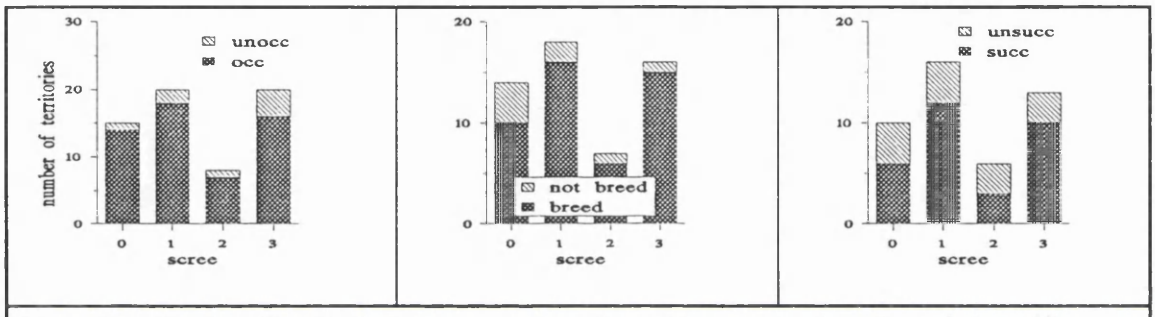

Figure 7.1g. Number of territories by occupancy, breeding, and success by class of scree below cliff.
scree 0 = none, 1 = some, but localised and old, 2 = substantial amount, but mainly old, 4= substantial amount of fresh rockfall.

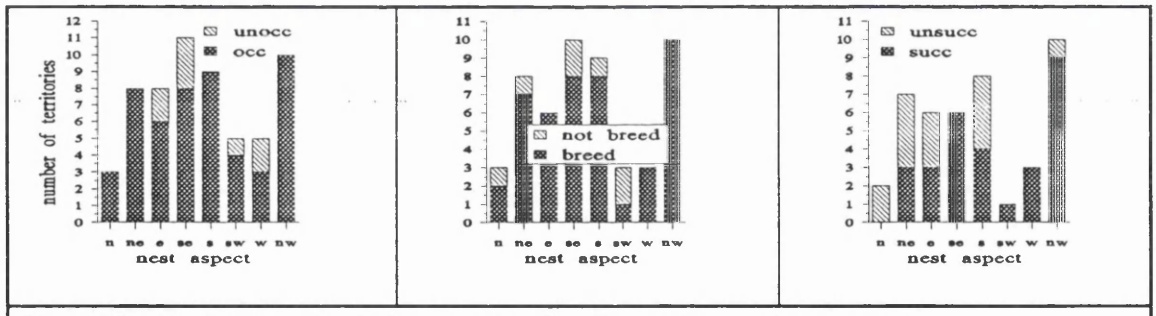

Figure 7.1h. Number of territories by occupancy, breeding, and success by nest aspect.

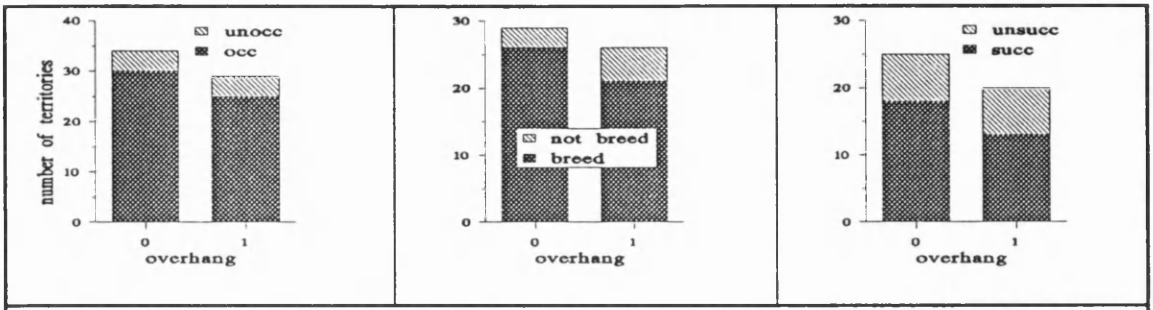

Figure 7.1i. Number of territories by occupancy, breeding, and success by presence or absence of overhang above nest.
overhang 0 = no, 1 = yes.

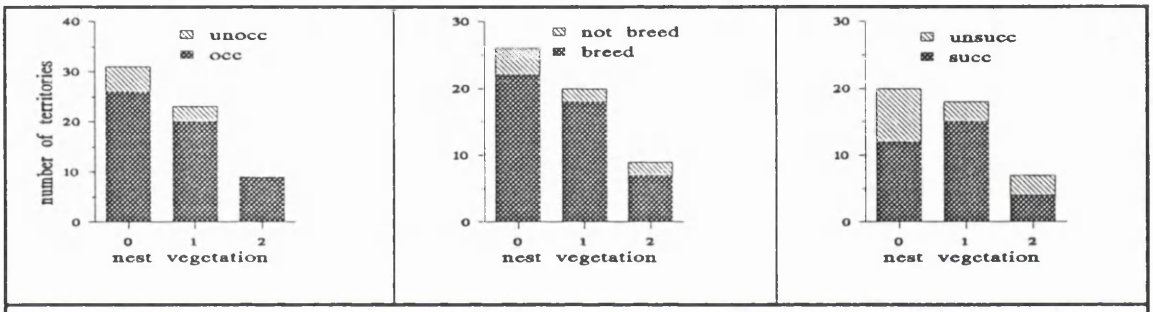

Figure 7.1i. Number of territories by occupancy, breeding, and success by class of vegetation at the nest.
vegetation 0 = none, 1 = sparse, 2 = heavily vegetated

variable (m)	occupied territories median (n)	unoccupied territories median (n)	U	p	sig.
cliff height	17.0 (55)	13.0 (8)	186.5	0.49	n.s
nest height	9.0 (55)	6.5 (8)	173.0	0.33	n.s
ledge length	1.0 (55)	1.5 (8)	172.0	0.30	n.s
ledge depth	0.5 (55)	0.65 (8)	151.5	0.15	n.s
height to roof*	1.0 (25)	1.0 (4)	40.5	0.53	n.s
altitude	122 (42)	219 (7)	145.0	0.95	n.s

Table 7.2a. Comparison of breeding site variables measured on a continuous scale between groups of occupied and unoccupied territories. Mann-Whitney U-test with 2-tailed probability, corrected for ties.
*where under overhang

variable (m)	breeding attempted	breeding not attempted	U	p	sig.
	median (n)	median (n)			
cliff height	19.0 (47)	13.5 (8)	154.0	0.42	n.s
nest height	10.0 (47)	6.5 (8)	158.5	0.48	n.s
ledge length	1.0 (47)	2.0 (8)	165.5	0.58	n.s
ledge depth	0.5 (47)	0.5 (8)	170.0	0.66	n.s
height to roof*	0.5 (21)	1.5 (5)	15.0	0.01	*
altitude	140.0 (36)	127 (7)	115.0	0.72	n.s

Table 7.2b. Comparison of breeding site variables measured on a continuous scale between territories where breeding was and was not attempted. Mann-Whitney U-test with 2-tailed probability, corrected for ties.
*where under overhang

variable (m)	successful breeding attempt	unsuccessful breeding attempt	U	p	sig.
	median (n)	median (n)			
cliff height	20.0 (31)	17.0 (14)	198.5	0.65	n.s
nest height	10.0 (31)	10.0 (14)	191.5	0.53	n.s
ledge length	1.0 (31)	1.0 (14)	155.5	0.12	n.s
ledge depth	0.5 (31)	0.3 (14)	160.5	0.15	n.s
height to roof*	0.5 (13)	1.0 (7)	31.0	0.23	n.s
altitude	83 (22)	222 (12)	86.0	0.10	n.s

Table 7.2c. Comparison of breeding site variables measured on a continuous scale between groups of successful and unsuccessful territories. Mann-Whitney U-test with 2-tailed probability, corrected for ties.
*where under overhang

variable (m)	r_s	p	sig.
cliff height	-0.24	0.23	n.s
nest height	-0.23	0.25	n.s
ledge length	-0.04	0.83	n.s
ledge depth	-0.29	0.14	n.s
height to roof*	0.17	0.18	n.s
altitude	-0.03	0.90	n.s

Table 7.2d. Spearman rank order correlation between continuous breeding site variables with fledged brood size of successful pairs.
*where under overhang

variable (yes, no)	occupied (yes, no)		breeding (yes, no)		successful (yes, no)	
	Fisher exact p	sig.	Fisher exact p	sig.	Fisher exact p	sig.
type: open cliff	0.67	n.s	1.00	n.s	0.24	n.s
type: cliff in gully	0.64	n.s	1.00	n.s	0.41	n.s
type: tree	1.00	n.s	0.38	n.s	1.00	n.s
cliff aspect n	1.00	n.s	1.00	n.s	1.00	n.s
" ne	0.58	n.s	1.00	n.s	0.18	n.s
" e	0.27	n.s	0.58	n.s	0.36	n.s
" se	0.27	n.s	0.33	n.s	0.29	n.s
" s	1.00	n.s	1.00	n.s	0.23	n.s
" sw	0.57	n.s	0.10	n.s	1.00	n.s
" w	0.43	n.s	1.00	n.s	0.54	n.s
" nw	1.00	n.s	1.00	n.s	0.47	n.s
view	1.00	n.s	0.38	n.s	0.53	n.s
nest aspect n	1.00	n.s	0.38	n.s	0.09	n.s
" ne	0.58	n.s	1.00	n.s	0.18	n.s
" e	0.27	n.s	0.58	n.s	0.36	n.s
" se	0.14	n.s	0.63	n.s	0.16	n.s
" s	0.59	n.s	1.00	n.s	0.23	n.s
" sw	0.51	n.s	0.05	*	1.00	n.s
" w	0.12	n.s	1.00	n.s	0.54	n.s
" nw	0.34	n.s	0.33	n.s	0.14	n.s
overhang	1.00	n.s	0.45	n.s	0.22	n.s

Table 7.3a. Fishers Exact Test for differences between binary breeding site variables grouped by occupancy, breeding and success.

variable	occupancy (*df* 1)		breeding (*df* 1)		success (*df* 1)		brood (*df* 4)	
	KW	p (sig.)	KW	p (sig.)	KW	p (sig.)	KW	p (sig.)
ledges	0.14	0.70 ns	2.99	0.08 ns	0.21	0.64 ns	2.16	0.70 ns
cliff veg.	0.05	0.82 ns	1.26	0.26 ns	3.11	0.08 ns	1.91	0.75 ns
cliff wet.	0.84	0.36 ns	0.18	0.67 ns	0.37	0.54 ns	1.05	0.90 ns
scree	1.48	0.22 ns	2.49	0.11 ns	0.28	0.60 ns	1.88	0.75 ns
nest veg.	1.13	0.28 ns	0.02	0.89 ns	0.39	0.53 ns	1.01	0.90 ns

Table 7.3b. Kruskal-Wallis one-way Analysis of Variance of ordinal breeding site variables and territories grouped by occupancy, breeding, success and fledged brood size.
occupancy, breeding and success = yes or no
fledged brood size, for successful pairs only, =1,2,3,4, or 6 chicks. There were no broods of 5 in the sample.

variable (yes, no)	brood = 1 or 2 (yes, no)		brood = 3 (yes, no)		brood ≥ 4 (yes, no)	
	Fisher exact p	sig.	Fisher exact p	sig.	Fisher exact p	sig.
type: open cliff	1.00	ns	1.00	ns	0.39	ns
type: cliff in gully	0.64	ns	1.00	ns	0.62	ns
type: tree	1.00	ns	0.42	ns	0.46	ns
cliff aspect n	1.00	ns	0.33	ns	0.37	ns
" ne	1.00	ns	0.58	ns	0.31	ns
" e	0.60	ns	1.00	ns	0.59	ns
" se	0.33	ns	1.00	ns	0.60	ns
" s	0.64	ns	1.00	ns	0.33	ns
" sw	0.29	ns	0.58	ns	0.58	ns
" w	0.50	ns	1.00	ns	0.50	ns
" nw	1.00	ns	0.16	ns	0.67	ns
view	0.58	ns	1.00	ns	1.00	ns
nest aspect n	1.00	ns	1.00	ns	1.00	ns
" ne	1.00	ns	1.00	ns	1.00	ns
" e	0.60	ns	1.00	ns	0.59	ns
" se	1.00	ns	1.00	ns	0.17	ns
" s	0.65	ns	1.00	ns	0.33	ns
" sw	1.00	ns	1.00	ns	0.58	ns
" w	0.58	ns	0.49	ns	0.54	ns
" nw	0.65	ns	0.60	ns	0.13	ns
overhang	0.32	ns	1.00	ns	0.49	ns

Table 7.3c. Fishers Exact Test for differences between binary breeding site variables grouped by fledged brood size.

CONCLUSIONS OF PART I

Nest-site features did not appear to influence occupancy, whether or not breeding was attempted, or breeding success. Comparison between groups for each variable showed a remarkable consistency in having no detectable influence. There were two exceptions to this: the height to nest overhang was significantly greater at sites where breeding was not attempted and there was also greater non-breeding at south-west facing nests. This may have reflected a choice against exposed positions, however: i) these birds did not go on to breed elsewhere; ii) neither of these variables detectably influenced breeding success or performance; iii) these sites had been used in previous years. It is therefore likely that these results were an artefact of a small data set compared to the number of univariate tests, and do not contradict the overall conclusion.

This analysis did not consider what characteristics ravens selected out of those available to them, and so I cannot use these data to predict which sites ravens would prefer in a given area. However I was able to define the minimum requirements for a site to be potentially suitable to hold a nest. It appeared that assessment of a site's potential to hold a raven nest in mid-Argyll need not consider many characteristics of the site. A minimum nest height of 2m was recorded, although most were considerably higher than this. Cliff nests were situated half way up the rock face, presumably to avoid predators approaching from above or below, therefore the minimum height of these should be at least 4m. In addition they should have a platform capable of supporting a nest at least at this height. Trees should have a configuration of branches capable of supporting a nest at a height of 2m or more. There was clearly a maximum altitude above which ravens were unlikely to nest; this is derived statistically in section 6.6c below.

PART II. IDENTIFICATION OF LOCATIONS WITHOUT POTENTIAL NEST SITES

OBJECTIVES

One of the principal objectives of part two of this thesis was to determine if suitable locations for ravens remained unoccupied in the study area. An obvious first step was to exclude all locations which were unlikely to hold ravens because of the absence of a potential nest site. A deductive approach was used to identify all GULs which were unlikely to contain potential nest site locations within the study area, using information given on published Ordinance Survey maps and in the Landsat derived map of landcover in the environment GIS.

METHODS AND RESULTS

Potential tree nest sites

Ravens may make use of trees in mixed and deciduous woodland, and mature plantation conifers (Davis and Davis, 1986; Dare, 1986; Elliot and Nuttall, 1983, Holyoak and Ratcliffe, 1968). In mid-Argyll only four nests

were found in trees, three in deciduous and one in a plantation conifer. The landcover at each of these locations was correctly given as deciduous or mature conifer plantation using the classified Landsat image on the GIS.

Potential cliff nest sites:

Examination of published Ordinance Survey maps showed that in 48 out of 50 cases open cliff nest sites were depicted on 1:50000 scale maps by a symbol representing 'cliff' or 'exposed rock' on very steep slopes. The two cliffs not so marked were substantial (15m and 30m), but were inexplicably omitted from the map. Cliffs in gullies were not shown on maps at this scale, but were depicted as 'rock' or 'waterfall' in the gully in 12 out of 12 cases on 1:25000 scale maps. All map features given these Ordinance Survey symbols across the entire GIS study area were digitised and incorporated into the GIS using methods described in Chapter 5.

Determining likely maximum altitude of potential raven nest sites

Ravens do not nest at the higher altitudes found within Britain. Ratcliffe (1962) found inland pairs to be most common in the altitude band 380 to 450m above sea level, uncommon above 600m, and never above 820m. In this study the highest nest found was at an altitude of 558m. Much ground lay at altitudes above 600m, which was clearly extremely unlikely to be occupied by ravens and which could be excluded from further consideration. Maximum altitude constraints were a possibility only at inland sites. Sites less than 0.5km from the coast were removed from the sample leaving 28 inland sites. The altitude of these sites had a normal distribution (Kolmogorov-Smirnov one sample test, $z = 0.56$, $p = 0.91$) with a mean of 251m (s.d. = 128m). In a normal distribution 99.7% of all observations fall within 3 s.d. of the mean. Thus, there was a 0.997 probability that all raven sites in the population were below 251+3(128) = 635m. This value was rounded down to 600m so that the classified altitude data set (100m classes) could be used. This altitude was taken as the cut-off above which ravens would be extremely unlikely ($p = 0.006$) to nest in the study area, using standard normal tables.

Classification of GULs on the basis of availability of potential nest sites and altitude

There were no areas of woodland or forestry above 600m. Using data extracted from the environment GIS, GULs (within 5km of the study area boundary) which contained either areas of broad-leafed woodland, mixed woodland or thicket forestry within their 500m grid cell were identified. These GULs were considered as **probably** containing a suitable tree nesting site for ravens. Those GULs not containing one of these land covers were considered **unlikely** to contain a potential tree nest (Figure 7.3).

Many cliffs and gullies occurred in the 53 GULs which had a minimum altitude of greater than 600m. All GULs which had a minimum altitude of $\leq$ 600m and also contained a cliff were considered as **probably** containing a suitable cliff nesting site for ravens. All GULs not so classed were considered **unlikely** to contain a potential cliff nest (Figure 7.4).

All GULs which were considered as not containing either a potential tree or cliff nesting site were identified and removed from the coverage of GULs on land to produce a new coverage containing only those GULs where nesting may potentially occur. Out of a total of 9677 GULs on land 5294 were identified as containing potential nest sites (Figure 7.5). Thus, using a GUL of 500m, 45% of the area could be excluded as potential locations for raven occupancy, solely on the basis of probable suitability for nesting .

Figure 7.3 Distribution of points centred in a 500m grid (GULs) which may have contained a potential tree nest site.
Potential tree nest sites (■) were considered to be all thicket plantation forestry, mixed and deciduous woodland shown on the GIS coverage of landcover. All other locations in the study area were considered unlikely to contain a potential tree nest site (□). Only intensive study areas are shown

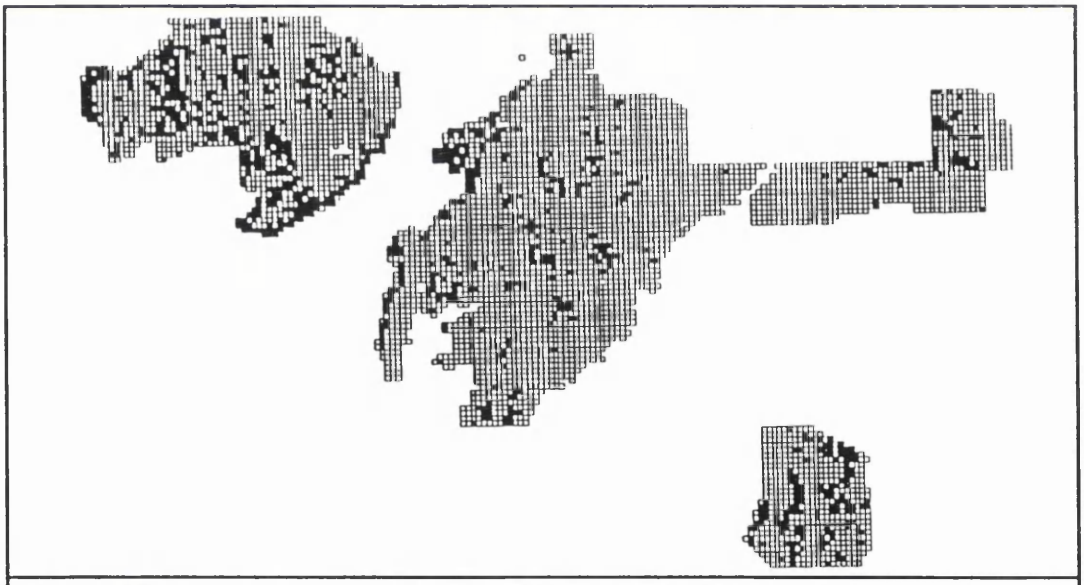

Figure 7.4 Distribution of points centred in a 500m grid (GULs) which may have contained a potential cliff nest site.
Potential cliff nest sites (■) were defined as locations ≤ 600m a.s.l. depicted on 1:50000 scale Ordinance Survey maps by a symbol representing 'cliff' or 'exposed rock' on very steep slopes, or depicted as 'rock' or 'waterfall' in a gully on 1:25000 scale Ordinance Survey maps. All other locations in the study area were considered unlikely to contain a potential cliff nest site (□). Only intensive study areas are shown .

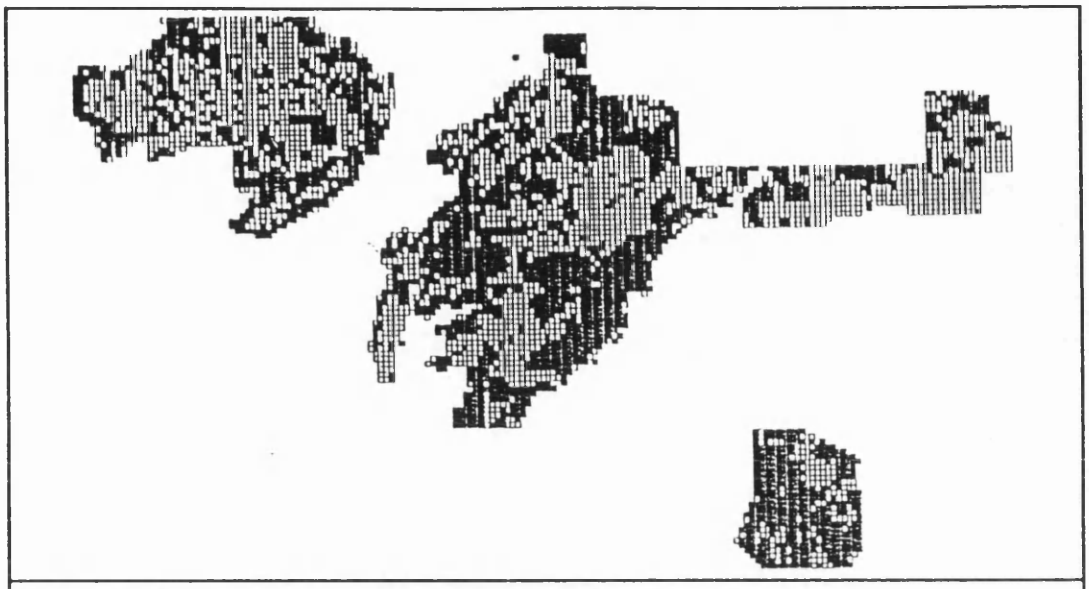

Figure 7.5 Distribution of points centred in a 500m grid (GULs) which may have contained a potential cliff or tree nest site (■).
Derived by combining values in coverages illustrated in Figures 7 .3 and 7.4 .

Predicting which cliffs would be preferred.

I attempted to use digital modelling of contour data (see Chapter 5) to predict cliff height, for instance by deriving fine scale slope and height difference (ruggedness) maps, using a variety of algorithms. I wished to find a method to rank all cliffs in the study area by height to refine models of raven distribution undertaken in subsequent chapters. These attempts failed and I do not include details of this work in this thesis. In summary I was able to predict whether cliffs would be very large (> 50m) or not, but I was unable to predict with sufficient accuracy cliff height below 50m, as this was the resolution at which original contours were digitised. I estimate that resolution to the nearest 10m would be required to distinguish cliffs at a suitable scale to rank preferences for ravens in mid-Argyll. It was not feasible to digitise contours to such precision, or, alternatively, make field inspections of enough sites over a wide enough area to be useful in this study.

Distribution of gaps and potential nest sites

The distribution of vacant locations was compared with the distribution of potential nest sites by performing attribute queries of the Arc/Info GUL polygon attribute table to produce summary information and maps. As cliffs were preferred to trees as nest sites, GULs which contained both cliff sites and tree sites were classed as cliff sites. The distribution of vacant GULs is mapped in Figure 6.3, chapter 6. Just under half of the GULs classed as vacant could be excluded as potential raven sites because they were extremely unlikely to contain a suitable nest site (Table 7.4). There were differences in the proportion of vacant GULs which contained nest sites between intensive study areas. These were due largely to a greater number of potential tree sites being available in COWAL and LORN (Table 7.4), and more potential cliff sites on MULL. Differences in the number of vacant potential tree sites were due to greater amounts of mature plantation forestry being available in COWAL and LORN (Table 7.5). The distribution of vacant GULs which also contained a possible cliff site, tree site only, and both are given in Figures 7.6 to 7.8.

intensive study area	total GULs	total vacant GULs	number of vacant GULs containing : ( ) = % of vacant GULs in study area containing: [ ] = % of all GULs in study area containing:		
			potential cliff nest site [1]	potential tree nest site only [2]	potential nest site [3]
COWAL	543	56	11 (20) [2]	35 (63) [6]	46 (82) [8]
GLENS	662	391	12 (3) [2]	101 (26) [15]	113 (29) [17]
LORN	2746	985	63 (6) [2]	579 (59) [21]	642 (65) [23]
MULL	1579	360	99 (28) [6]	51 (14) [3]	150 (42) [9]
Total	5530	1792	185 (10) [3]	766 (43) [14]	951 (53) [17]

Table 7.4 Availability of potential nest sites in vacant GULs
[1] may have also contained potential tree nest site
[2] did not contain potential cliff nest site
[3] tree and cliff sites combined

intensive study area	number of vacant GULs containing potential tree nest sites by woodland type ( ) = % of vacant GULs containing potential tree nest sites in study area[1] [ ] = % of all GULs in study area[1]		
	native woodland only [3]	mature plantation forestry only	both native woodland & mature plantation forestry
COWAL	2 (6) [< 1]	31 (89) [6]	2 (6) [< 1]
GLENS	29 (29) [4]	65 (64) [10]	7 (7) [1]
LORN	136 (23) [5]	383 (66) [14]	60 (10) [2]
MULL	37 (73) [2]	10 (20) [1]	4 (8) [< 1]
Total	204 (27) [4]	489 (64) [9]	73 (10) [1]

Table 7.5 Woodland type within vacant GULs containing potential tree nest sites only

[1] see Table 7.4

[2] Mixed woodland and deciduous woodland

Figure 7.6 Vacant 500m grid cells (GULs) in intensive study areas also potentially containing a cliff nest site (■)

Figure 7.7 Vacant 500m grid cells (GULs) in intensive study areas also potentially containing a tree nest site (■)

Figure 7.8 Vacant 500m grid cells (GULs) in intensive study areas also potentially containing a cliff or tree nest site (■)

CONCLUSIONS OF PART II

Classification of GULs containing potential nest sites based on the Landsat and Ordinance Survey derived GIS coverage of landcover, or symbols on 1:50000 and 1:25000 Ordinance Survey maps will have missed some sites, such as isolated trees and some rock-faces. However, on the basis of known nest sites in the study area, the classification of GULs for potential nest sites correctly identified 96% of raven sites. This was a higher success rate than could realistically be expected through more complex statistical analyses of terrain and landcover variables extracted from the GIS. It should be emphasised that the point of this analysis was to exclude the many areas where ravens could not nest because of the extremely low likelihood of a suitable nest site being present. This did not mean that all those remaining actually contained suitable nest sites, but rather that some 96% of all raven sites in the population were contained in this sample. This served as a first filter in identifying potential raven sites throughout the study area. Field records were required to confirm the suitability of potential nest-sites within GULs identified as probably containing a nest site. This is done after further filtering based on the suitability of the surrounding habitat described in the next chapters.

Only 10% of vacant GULs were also classed as potentially containing a cliff nest-site. In a few areas the lack of cliff-sites may have influenced raven distribution (as these were the preferred nest-site type), however in most aggregations of vacant GULs some cliffs were present. A further 43% of vacant GULs potentially contained tree sites. Thus, although many GULs could be eliminated as potential nesting areas, nest-sites were not likely to limit raven numbers in most parts of intensive study areas. I estimated the number of 'missing' raven territories using the methods given in chapter 6. Considering only vacant GULs potentially containing cliff-sites I estimated that MULL could support a further 13 sites, COWAL 3, GLENS 9, and LORN 18. On this basis the population in these study areas was only 55% of the maximum. Many more missing sites would have been added if GULs potentially containing tree-sites had been included.

DISCUSSION

Solonen (1982) defined two types of nest site selection in birds: 'eurytopic' species are able to utilise a wide variety of sites whereas 'stenotopic' birds have very specific requirements. Ravens clearly fall into the first

category. Though they exhibit an obvious preference for certain sites given a choice (Ratcliffe, 1962), many other situations are used. Hollyoak and Ratcliffe (1968) report nests in very small trees 'little more than bushes' in some areas. Booth (1979) found one tree nest only 1.8m above the ground and another at 2m on a 4m cliff. Nests occur on stream and river banks (Booth, 1979; Davis and Davis, 1986) and there are many records of them breeding on buildings. Cochet and Faure (1987) reported an unusual nesting site on a tall (and very exposed) electricity pylon in the Massif Central.

Nest-site selection

In this study I did not examine site choice by statistically comparing sites used by ravens with those available to them. Nor to my knowledge has this been attempted elsewhere. However it was my impression that small cliffs (<10m) and trees were used only where there were no tall cliffs in the vicinity. Where there were no cliffs or trees, for example at three sites on Tiree, nests were placed on inward sloping rock faces less than 3m high, which could be easily reached by humans without climbing. These observations are consistent with other studies.

Tall cliffs appear to be universally preferred. On three British archipelagos sea cliffs were more heavily used than inland crags (Cowin, 1941; Booth, 1979; Ewins et al, 1986), though this probably reflects their greater height. Nogalez (1991) found 68% of *C.c. tingitanus* nests on inland crags and only 22% on sea cliffs on the island of Hierro (Canary Archipelago) probably because inland crags were taller. Where cliffs are in short supply, trees are frequently resorted to. In central Wales, Davis and Davis (1986) found 71% of all nests in trees. Dare (1986) found only 3% of nests were in trees in Snowdonia but 60% in Migneint-Hiraethog. This reflected the greater availability of cliffs in Snowdonia. Tree nesters in both studies showed an apparent preference for conifers. This may have been due to their greater height, however branch architecture suitable for nest placement may also play a part (Loman, 1975).

Ravens appear to show no preference for aspect in any region, even where cold or heat stress might be thought to be important, or where rainfall is heavy and wind from a prevailing direction (Allin, 1968; Dare, 1986;

Ratcliffe, 1962; Poole and Bromley, 1987;. Nogalez, 1991). Perhaps the deep and well lined nest of the raven provides sufficient protection from the elements. Additional shelter may be sought as many authors have noted the apparent preference for nesting under overhangs (Ratcliffe, 1962; White and Cade, 1971; Poole and Bromley, 1987; Hooper, 1977), however, this may rather be to deter predators. Cliff structure, and hence availability and structure of nest placements, is dictated by geology. If certain ledge structures are preferred by ravens one may expect selection for certain types of rock where there is a choice in a nesting territory. I did not observe any in mid-Argyll (in several sites alternative nests were placed on different rock types) and Hooper (1977) found that use of cliff sites of a particular type was proportional to their abundance.

Thus ravens appear to select the tallest nest site available to them, and preferably under an overhang. In the terrain where most populations are found, cliffs provide taller, better protected locations and are preferred to trees. This is not a hard and fast rule however, as some pairs may have both cliff and tree sites as alternatives (A.C. Cross pers.comm.). Apart from these considerations, most sites appear to be sufficient so long as they have some feature capable of supporting a nest, and even where preferred sites are unavailable, breeding will be attempted on very minimal platforms: low to the ground and exposed.

Effect of site selection on breeding performance

Breeding performance was not influenced by features of the nest-site in mid-Argyll in 1990. The evidence of this study and others suggests that ravens choose their nest site solely to minimise the risk of predation, and that shelter from the elements is unimportant as this is provided by the nest. The main predator of ravens in Britain is man, with very occasional raids on accessible nests by foxes (Ratcliffe, 1962). In both cases, attacks usually result in complete destruction of the clutch/brood. Thus regional differences in nest-site quality may be expected to influence the proportion of breeding attempts which were successful, but not the number of young fledged by successful pairs. The vulnerability of nests to predation will vary with the pressure from humans, and perhaps the presence of foxes. In mid-Argyll there was little evidence of human disturbance in any area (Chapter 2). There was however circumstantial evidence that minimum nest cliff heights were influenced by the presence of foxes. When nest site descriptions from Tiree were added to the data presented in this chapter,

a total of 11 nest cliffs under 10m high were recorded. Of these, four were on Mull, four were on Tiree (both islands were without foxes) and only two were on the mainland (foxes common). This does not however take into account the relative availability of taller cliffs in these regions.

Davis and Davis (1986) found no difference in the success of nests built in trees or on cliffs. There was however some indication that nests did better in taller trees than those in smaller ones. This was probably due to greater exposure to predation and deliberate human disturbance in small trees. In this region human predation was the predominant cause of failure (egg collecting and destruction of the nest accounted for 89% of all known causes of failure, and 43% of all nests which failed). Throughout Britain Hollyoak and Ratcliffe (1968) thought that breeding success tended to be higher on taller cliffs, again due to increased protection against predation. In Orkney, inland sites were more accessible than sea cliffs (Booth,1979). Here there were higher failure rates at inland sites, due to human interference, but there was no difference between the number of young produced by successful pairs in either area.

Conclusion

Though observations indicated that ravens mid-Argyll choose sites that offered the best protection against man and occasional carnivores, a great range of site types were used. Minimal specifications were required to give a high probability that a GUL (grid unit of location, Chapter 5) contained at least a site capable of supporting a nest a few metres above the ground, and therefore satisfying minimum nest-site requirements. I emphasise that this was not tested directly but by predicting raven occupancy of GULs in the following chapters. The main purpose of this chapter was to determine the influence of nest site quality on raven distribution and breeding performance. There was no evidence that nest site quality affected occupancy or breeding performance in the study area. Thus, models of raven breeding performance presented in Chapters 8 and 9 did not need to take this into account.

Gaps in the distribution of ravens in mid-Argyll could not be explained by a lack of potential nest-sites, except for a few locations. Considering the rugged nature of the study area this is not surprising. A similar analysis in

other areas such as the Southern Uplands, where the hills have fewer rock outcrops, may show that distribution is limited by nest-site availability. However, given the raven's catholic choice of sites and apparently minimal requirements, nest-site availability is unlikely to influence population density in most areas of Britain. The distribution of preferred sites may however strongly influence traditional distributions within an area.

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CHAPTER 8. DETERMINING SUITABLE CONDITIONS FOR RAVEN OCCUPANCY

INTRODUCTION.

When ecologists examine habitat choice or suitability for an animal, they commonly look for differences in habitat between groups of locations where it occurs at different densities (often presence or absence), or where different activities take place. When applied to the distribution of an animal, the comparison of habitat between occupied and unoccupied locations makes the implicit (but usually untested) assumption that the population occupies all suitable habitat. That is, that the carrying capacity of the study area for the species has been reached, and that locations in which the animal does not occur are in unsuitable habitat. Where breeding animals are territorial and suitable habitat limited, a surplus of non-breeding but mature adults (floaters) may build up once the maximum number of territories capable of being supported has been reached.

There were apparently few floaters in mid-Argyll (see Chapter 4), and there were many areas which seemed to the eye suitable for ravens but were vacant. For these reasons the assumption that raven distribution in mid-Argyll was limited by suitable habitat was considered unreasonable. In addition, Hobbs and Hanley (1990) provided a strong theoretical argument that animal distributions will reflect carrying capacity only under a set of conditions which are rarely met in nature. One of these was that environmental conditions permit long-term, stable equilibria between the animal population and limiting resources. Given the apparent disruption of stable populations of ravens by rapid change in upland land-use (Chapter 1), and the extensive and continuing rate of these changes in mid-Argyll, this condition was obviously not met.

Therefore, in this thesis I make a distinction between ground which was occupied by ravens and ground which was vacant because it is a) unsuitable or b) suitable but ravens were absent for reasons unknown or unmeasured. In the two previous chapters I identified all GULs which potentially contained a nest site, and all GULs situated in gaps in the distribution of ravens within the intensive study areas. These maps were

combined to identify all vacant locations which potentially contained a nest site. Of those which remained some were probably unsuitable because they were centred in poor habitat. At the outset the differences between suitable and unsuitable habitat were unknown. However, previous studies of ravens and land use change, described in detail in Chapter 1, had identified afforestation with conifer plantation and agricultural improvement as adversely affecting the suitability of sites for ravens. These land covers therefore seemed a reasonable basis for an initial classification of habitat suitability. In addition I examined the distribution of raven nests in relation to roads and buildings, as some otherwise suitable locations may have been avoided because of the proximity of human activities.

Ravens probably have large home ranges. I have observed individuals flying in a direct line from their nests till they flew out of sight after 5km (mid-Argyll) and 7km (west Eire). Consequently, when examining the effect of land-use change on breeding performance, large areas must be considered. However, nest site location will probably be more strongly influenced by landscape closer to the nest. Marquiss et al. (1978), investigating raven populations at densities similar to that in mid-Argyll, found breeding performance to be chiefly associated with the extent of afforestation within 5km of the nest, whereas occupancy was most closely associated with afforestation within 3km. In this chapter I therefore restricted the analysis to afforestation and agricultural improvement within 3km. Within this area, loss of foraging habitat may have a greater impact the closer to the nest it occurs as there are costs in foraging over greater distances (Davies and Houston, 1984). I therefore adopted a data design which incorporated variance due to the spatial distribution of habitats within the area surrounding the nest.

Lawton and Woodroffe (1991) used multivariate techniques to distinguish apparently suitable but unoccupied habitats from unsuitable habitats for breeding colonies of bank voles (*Arvicola terrestris*). I used their approach for the same purpose in this study, but extended the analyses not only by incorporating the spatial distribution of habitats around sites, but also by a novel use of GIS in the statistical analysis which enabled me to deal with a large number of cases.

METHODS

Data extraction and preparation

A Lites2 macro was written to measure the amount of each class of landcover in specified regions around specified locations from the classified landcover raster layer of the Horizon GIS. The total area in each landcover class was extracted in square windows of increasing size for each GUL in the GIS study area. The length of sides for windows were 0.5km, 1.0km, 2.0km, and 3.0km. Bearing in mind that half the mean nearest neighbour distance was 1.8km (Table 4.8) , these areas correspond to increments from well within the territory up towards the outer regions of the likely home range, thus meeting the requirements set out in Section 5.10. Results were sent to text files and imported into DBase4. For each window, with the exception of 0.5km, the amount of landcover in each class in the total window size below was subtracted and saved as a new data file. This produced a series of nested squares which could be added to give a total for the largest window. This form of the data is illustrated in Figure 8.1 below. This data design allowed the analysis to treat each landcover category in each nested square as a separate variable, thus taking account of the spatial distribution of land covers around GULs.

Values in nested squares were combined into a single data file which contained 48 landcover variables (4 nested squares x 12 landcover classes in each) for each of the 9677 GULs. The amount of land in each nested square in each GUL was calculated by summing all landcover classes except class 1 (unclassified), class 11 (fresh water) and class 12 (sea). Four different types of landcover were defined (see Chapter 5 for a definition of landcover classes) :

mature coniferous forestry plantation (landcover class 2)

pre-thicket conifer plantation / scrub (landcover class 3)

agriculturally improved fields (landcover class 7)

semi-natural vegetation (sum of landcover classes 4, 5, 6, 8, 9 and 10)

These four categories were transformed into proportions of land within each nested square. This was required to remove the variance in differences in landcover due to different amounts of water within nested squares and also standardised values from nested squares of different sizes.

As the objective of the analysis was to determine which GULs were located in habitat suitable for occupancy, those GULs which were unlikely to contain a potential nest site were excluded, leaving 5294 cases.

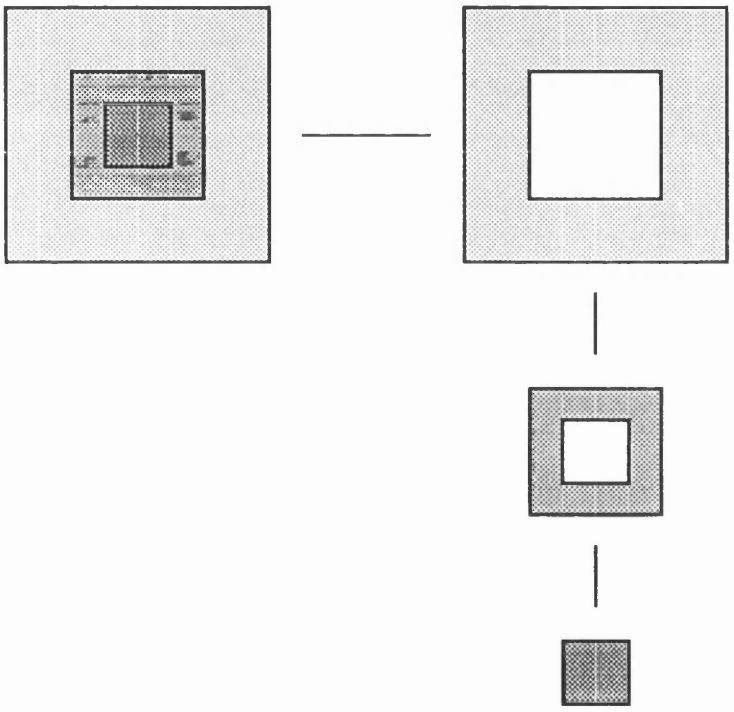

Figure 8.1 Creating "nested squares" of amount of land cover class in increasing distance from the centre of a GUL.
In the top left a window of 2km is shown. From this the corresponding window of 1km was subtracted leaving just the amount of area covered by each class in the range >1km to ≤2km nested square. From the total coverage in the 1km window (centre right) the values in the corresponding 0.5km window (bottom right) were subtracted leaving just the amount of coverage by each class in the range >0.5km to ≤1.0km nested square. This process was performed on windows from 3km to 0.5km leaving four nested squares.

Analysis

Principal component analysis

A principal component analyses (PCA) was performed using the Genstat 5.2 statistical package on a PC (Genstat 5 committee, 1989) to reduce the data into components of total variance. The Genstat 5 package was

used as it had the capacity to handle the very large data sets required, and permitted greater control over analysis and output than the SPSS PC+ package used elsewhere in this thesis. Data were left as proportions because PCA used descriptively, as in this case, makes no assumptions regarding the distribution of variables (Tabachnick and Fidell, 1989, page 603; Digby et al, 1989, page 90) and untransformed data greatly eased interpretation of principal components. I took principal components of the sums of squares and products matrix rather than the correlation matrix, as the objective was to summarise the variance into a small number of components rather than describe relationships between variables.

Principal component loadings were derived from a subset of data (974 cases), restricted to GULs in intensive study areas which were classed as 1) vacant and containing a potential nest site, or 2) were occupied in 1990. This was done to increase the chance of producing orthogonal components of variance which were useful in estimating land cover suitability for ravens, as the data input was restricted to those cases where ravens were present and those where they could have been, based on distribution and nest site availability. Principal component loadings derived from larger data sets (including locations where raven distribution was unknown or where ravens could not have been based on known distribution and nest-site availability) were likely to be less useful as the analysis would take account of extra variance in the data which did not pertain to the observed distribution of ravens and vacant locations. Principal component scores were calculated for all 5294 cases from the loadings calculated from the 974 case subset.

Estimating habitat suitability based on principal component scores

The mean value of the principal component scores of occupied GULs in the intensive study areas were compared with those values for vacant GULs in intensive study areas. Principal component scores were often non-normally distributed (tested using Anderson Darling and Cramer von Mises tests in Genstat) but the sample sizes permitted the use of z tests for differences in means (Fowler and Cohen, 1990, page 174). Those principal components which differed between occupied and vacant groups at the 5% level were retained for further analysis.

The scores of pairs of different retained components could be plotted against each other as Cartesian x,y coordinates. I wished to identify all GULs which fell within the hyper polygon in multi-dimensional principal component space defined by GULs containing occupied ravens sites in 1990. That is to say, that a particular GUL from the overall GUL population would be considered suitable for occupancy if, when plotted on a multidimensional plot of principal component scores, it fell within the cloud of points obtained by plotting GULs containing occupied raven sites. This was best done as a set of 2-dimensional calculations by considering each pair of principal component scores separately, and identifying all cases falling within or on the 2-dimensional polygon surrounding occupied GULs. With a small number of cases such operations can be performed by plotting out cases labelled with case identifiers and noting the position of each (e.g. Lawton and Woodroffe, 1991). However this was unfeasible with the thousands of cases used in the present analysis and no statistical or graphics computer package available to me permitted selection of cases through a graphic interface. The problem, which may be quite common in many numerical analyses, was relatively straight forward when viewed as one of mapping overlapping distributions. Consequently, I used PC Arc/Info GIS package to map the distribution of principal component scores for all pairs of retained principal components, by inputting x,y coordinates for each point as a map coordinate. The coordinates were obtained from the text file of principal component scores, output by Genstat. Separate files were created for occupied GULs (52 cases) and all others (5242 cases). These were imported to Excel 4 (a high capacity spreadsheet) where pairs of components were matched and output as text files. These were edited in a programmable text editor (Boxer) into a form suitable for input as point text data for map creation in Arc/Info. The Arc/Info procedure 'generate' was used to create new coverages. Thus, separate coverages were made of scores of each pair of retained principal components for i) GULs containing an occupied raven site in 1990 and ii) all others (not occupied) which potentially contained a nest site. Because these data were geographically referenced (in this case in principal component space) coverages could be overlaid.

Each coverage for occupied GULs was edited in Arc/Info module 'Arcedit'. A polygon was digitised which formed a convex hull around the cloud of points, that is, the largest area possible enclosed by a polygon made by joining points with straight lines. Polygon topology for the new polygon coverage was made using Arc/Info

procedures 'clean' and 'build'. The coverage of all non-occupied points for a particular pair of principal components was overlaid with the respective occupied polygon. All points lying within or on the boundary of the polygon were within observed limits suitable for raven occupancy for that particular pair of principal components. This was repeated for all possible pairs of principal components. Those GULs which were found to be within limits suitable for raven occupancy in every case (or, more formally, lay within or on the hyper convex hull) were deemed to be centred in habitat suitable for occupancy when considering afforestation and agricultural improvement only.

RESULTS

Principal Component Analysis

The first six principal components, which explained nearly 97% of the total variance (Table 8.1), were retained for analysis. Loadings for these components are given in Table 8.2 and illustrated in Figure 8.1a-f. Principal component ONE explained 66.9% of the variance in the data set and was concerned primarily with the amount of mature forestry and semi-natural vegetation in nested squares around the GUL. Mature forestry had high negative loadings, with greater negative weight applied to smaller nested squares, whereas high positive loadings were applied to semi-natural vegetation, with greater positive weight applied to smaller nested squares. Smaller negative loadings were applied to the proportion of pre-thicket/scrub with almost equal weight for each nested square. The proportion of land agriculturally improved made a negligible contribution. Thus the proportions of semi-natural vegetation and mature forestry pulled in opposite directions. GULs surrounded by greater amounts of mature forestry at the expense of semi-natural vegetation had lower scores than those with little mature forestry, especially if it was close to the GUL.

Principal component TWO explained some 9% of the total variance. This component reflected the amount of pre-thicket/scrub relative to mature forestry, with emphasis on areas closer to the GUL. High negative loadings were applied to the proportion of land covered by pre-thicket/scrub, with reduced negative weighting with increasing nested square size. High positive loadings were applied to the proportion of land covered by mature

forestry with reduced positive weightings with increasing nested square size (becoming slightly negative at 3km nested square). The smaller contribution to the score by the proportion of semi-natural vegetation was positive, and increased with larger nested squares. The proportion of land agriculturally improved made a small negative contribution to the score applied in relatively even measure to each nested square.

Principal component THREE explained some 12% of the total variance. This component took account of the distribution of mature forestry and semi-natural vegetation around the GUL. The variables pre-thicket/scrub and agriculturally improved land made small contributions to the score which was dominated by semi-natural vegetation (highly negative at 1km and below, but highly positive above for regions outside these)and mature forestry (small loadings at 1km and below, but highly negative for regions outside this). Thus a GUL with lots of mature forestry in 2km and 3km nested squares but with little forestry and a high proportion of semi-natural vegetation in regions below these would have a large negative score whereas the opposite case would result in a high positive score. GULs with little forestry and/or semi-natural vegetation would have scores closer to zero.

Principal component FOUR explained 5% of the total variance, and explained the variance due largely to the proportion of land agriculturally improved, with greater amounts (especially within 2km) leading to high negative scores, and the proportion of pre-thicket/scrub with greater amounts within 2km leading to high positive scores. Smaller, positive contributions to the score were made by the proportion of land covered by semi-natural vegetation in each nested square. Thus, GULs with greater amounts of improved farmland around them obtained large negative scores; GULs with greater amounts of pre-thicket/scrub around them obtained large positive scores; and GULs with neither or both obtained scores closer to zero.

Principal component FIVE explained only 2% of the total variance, but was useful because, like component THREE, it took account of variance due to the distribution of mature forestry and semi-natural vegetation around the GUL. In this case however, the distinction was not between near or far from the GUL, but rather the middle ground versus near and far. GULs with much mature forestry at 0.5 - 2km but semi-natural

vegetation in regions above and below this obtained large negative scores, whereas those with *vice versa* obtained high positive scores.

Principal component SIX explained nearly 2% of the total variance. All landcover types contributed to the score, and the loadings were difficult to interpret. The largest positive contributions were from pre-thicket/scrub in regions over 1km from the GUL. Equally large negative contributions were from mature plantation in regions over 1km from the GUL.

principal component number	summary land cover types contributing to the score (↓) = increase in landcover contributes to low scores (↑) = increase in landcover contributes to high scores	% variance explained
ONE	amount of mature plantation (↓) & semi-natural vegetation (↑)	66.9
TWO	amount of pre-thicket/scrub (↓) relative to mature plantation (↑)	12.1
THREE	distribution of mature plantation (near = ↑, far = ↓) & semi-natural vegetation (near = ↓, far = ↑)	9.1
FOUR	proportion of pre-thicket/scrub (↑) and agricultural grassland (↓)	5.0
FIVE	distribution of mature forestry 1-2km distant (↓) and semi-natural vegetation (↑)	2.0
SIX	mixture of land covers	1.7
Total		96.8

Table 8.1 Principal components analysis: % total variance explained by the first 6 principal components

proportion of landcover type in total area of land	nested square	principal component number					
		ONE	TWO	THREE	FOUR	FIVE	SIX
pre-thicket/scrub	0.5km	-0.1160	-0.4656	0.1836	0.4167	-0.0369	-0.2343
mature forestry	0.5km	-0.3767	0.5117	0.1687	0.0467	0.4008	0.2022
improved agric.	0.5km	0.0138	-0.1247	0.1327	-0.4910	-0.0356	-0.2524
semi-natural	0.5km	0.4791	0.0790	-0.4839	0.0267	-0.3286	0.2825
pre-thicket/scrub	1km	-0.1095	-0.3809	0.1134	0.2960	-0.0461	0.1547
mature forestry	1km	-0.3445	0.3901	-0.0498	0.0789	-0.3883	0.0299
improved agric.	1km	0.0155	-0.1239	0.1327	-0.5005	-0.0434	-0.1246
semi-natural	1km	0.4389	0.1144	-0.1967	0.1246	0.4784	-0.0584
pre-thicket/scrub	2km	-0.1037	-0.1966	-0.0236	0.0706	0.0793	0.4261
mature forestry	2km	-0.2438	0.0829	-0.3669	0.0604	-0.2694	-0.2794
improved agric.	2km	0.0165	-0.0921	0.0864	-0.3216	0.0126	0.1350
semi-natural	2km	0.3316	0.2057	0.3041	0.1900	0.1772	-0.2824
pre-thicket/scrub	3km	-0.0914	-0.1324	-0.0789	-0.0065	0.1470	0.3481
mature forestry	3km	-0.1830	-0.0406	-0.4196	0.0378	0.2260	-0.4566
improved agric.	3km	0.0115	-0.0616	0.0591	-0.2065	0.0285	0.1635
semi-natural	3km	0.2626	0.2337	0.4399	0.1737	-0.4013	-0.0544

Table 8.2 Variable loadings for the first six principal components
Variables were proportions of total area of land occupied by four types of landcover in each nested square (see Figure 8.1)

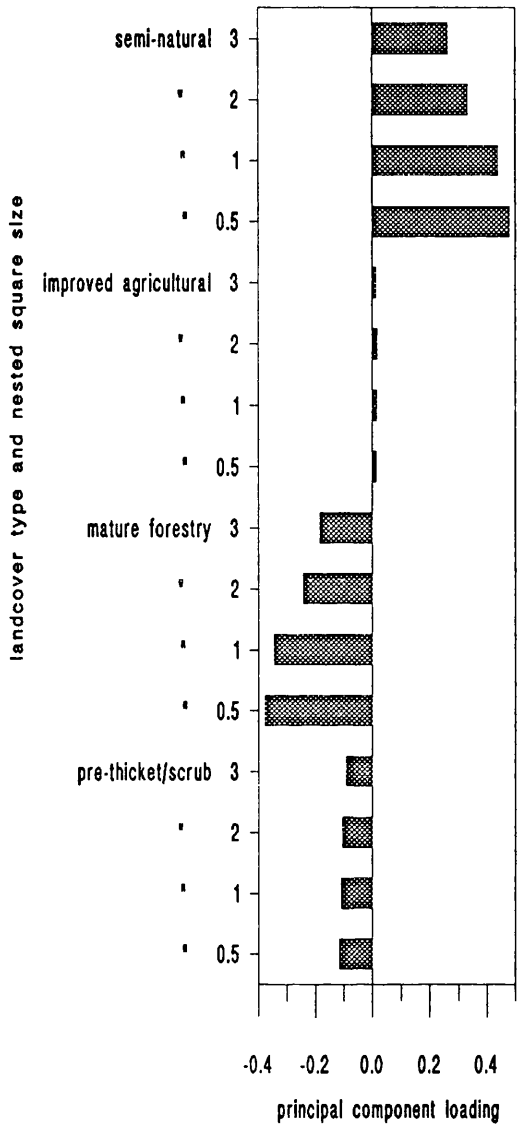

Figure 8.1a. Variable loadings for principal component ONE

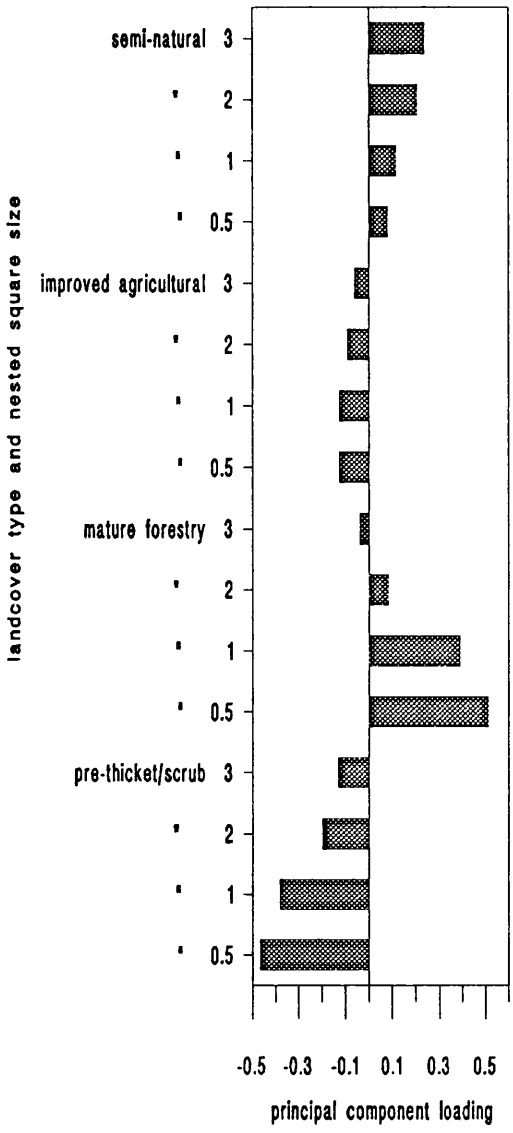

Figure 8.1b. Variable loadings for principal component TWO

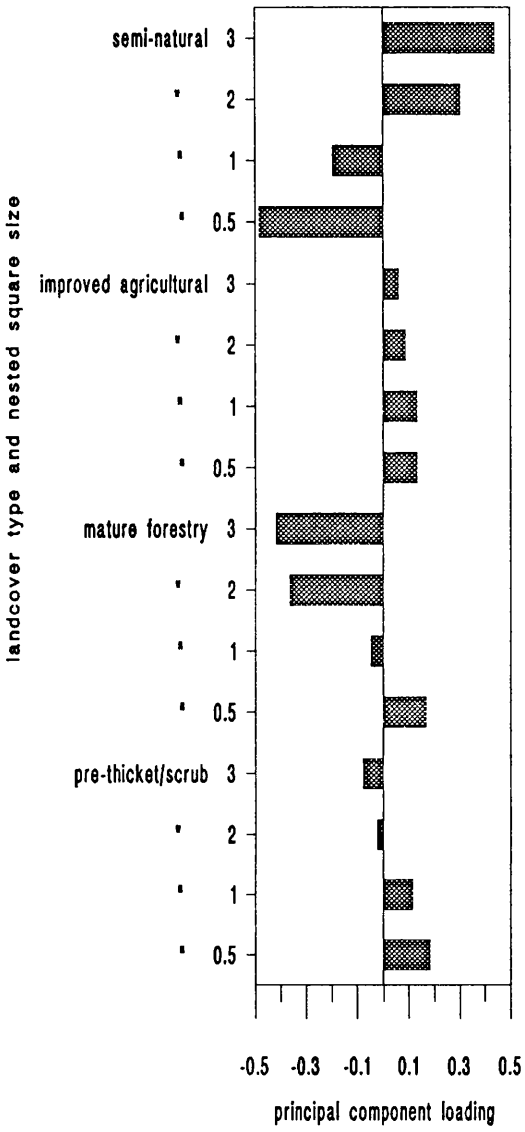

Figure 8.1c. Variable loadings for principal component THREE

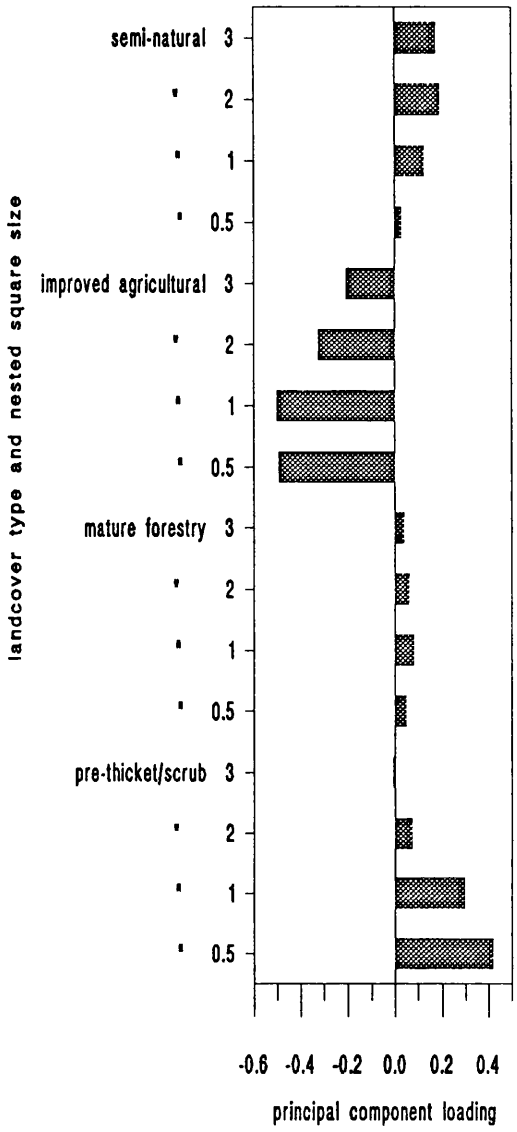

Figure 8.1d. Variable loadings for principal component FOUR

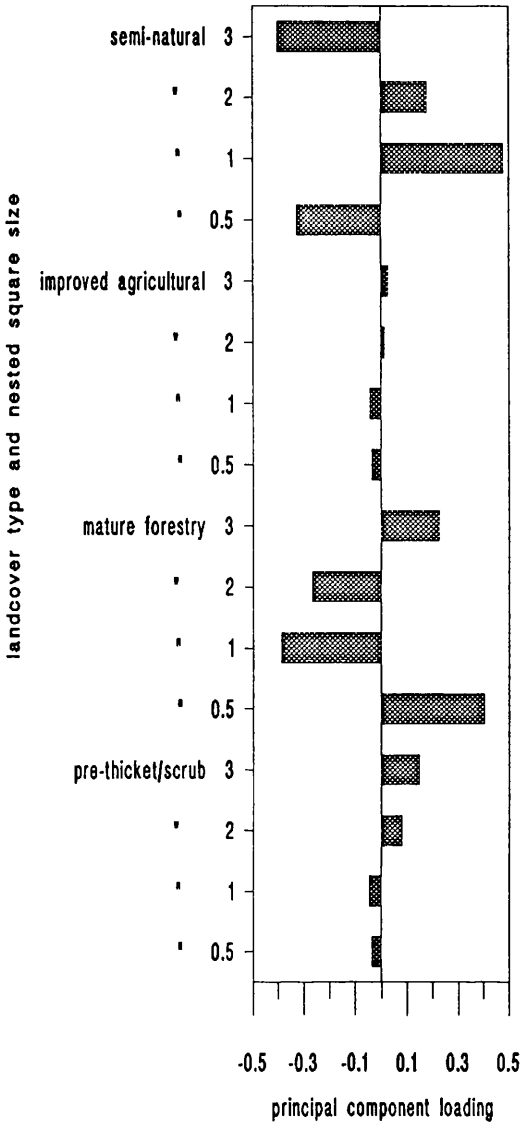

Figure 8.1e. Variable loadings for principal component FIVE

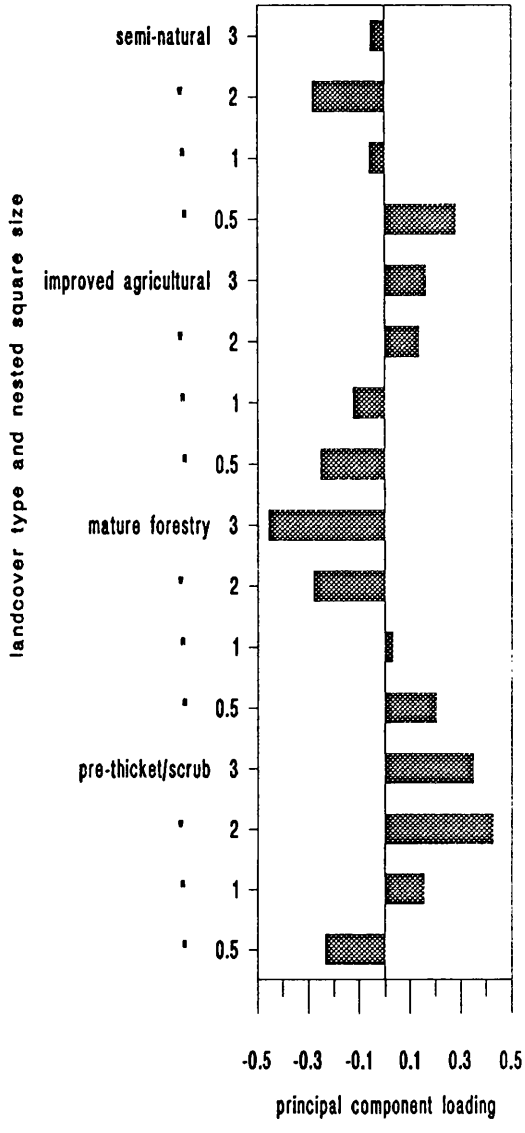

Figure 8.1f. Variable loadings for principal component SIX

Estimating habitat suitability based on principal component scores

The mean score and sample variance for each principal component is given in Table 8.3 for GULs occupied and vacant, but containing a potential nest in 1990. Results of *z* tests for differences in means between these two groups are given in Table 8.4. The mean score for occupied GULs was significantly higher than vacant GULs for principal components ONE, TWO and FIVE. These components were therefore considered useful in determining the suitability of the ground in which a GUL was situated for raven occupancy. The mean scores

for occupied and vacant GULs for the remaining principal component differences were not significantly different, and were therefore not useful for distinguishing habitat suitability for ravens.

principal component number	GULs containing a raven site occupied n = 52		GULs vacant but potentially containing a nest site n = 922	
	mean score	s.d.	mean score	s.d.
ONE	0.700	0.144	-0.039	0.503
TWO	0.060	0.043	-0.003	0.095
THREE	0.030	0.039	-0.002	0.071
FOUR	0.012	0.032	-0.001	0.039
FIVE	0.029	0.006	-0.002	0.016
SIX	0.018	0.012	-0.001	0.013

Table 8.3 Mean principal component scores of GULs occupied and GULs vacant in 1990.

principal component number	*z*	2-tailed p	sig.
ONE	-12.85	>0.000	***
TWO	-2.06	0.0194	*
THREE	-1.11	0.134	ns
FOUR	-0.48	0.315	ns
FIVE	-2.65	0.004	**
SIX	-1.18	0.119	ns

Table 8.4 *Z* tests for differences in means of PC scores for GULs occupied or vacant in 1990.

A convex hull was drawn around the cloud of occupied GULs mapped in each two dimensional combination: coordinates for each GUL for principal component ONE versus TWO, ONE versus FIVE, and TWO versus FIVE. These were laid over the equivalent distribution of non-occupied GULs containing a potential nest site. These distributions are illustrated in Figures 8.2a-c.

GULs which lay outside all three convex hulls were considered unsuitable for raven occupancy. In the first dimension (principal component ONE) occupied GULs had higher scores (less mature forestry and/or more semi-natural vegetation) than many non-occupied GULs. In the second dimension (principal component TWO) very high scoring or very low scoring non-occupied GULs were excluded. As this component related mainly to the mixture of pre-thicket and mature forestry, extreme values were found in more heavily afforested areas, whereas ravens occupied less afforested ground with scores consequently in the mid-range. Low values indicated high levels of pre-thicket relatively close to the GUL, however most cases were excluded because they had too high a score, indicating mature forestry near to the GUL. Similarly in the third dimension (principal component FIVE) the range found in scores of occupied GULs did not include high or low values because this component explained residual variance due to the spatial distribution of mature forestry relative to semi-natural vegetation: occupied GULs tended to have lower proportions of land under mature forestry and consequently had scores in the mid range. The amount of mature forestry in areas outside the 1km square did not appear to influence raven occupancy if areas within this had little afforestation (principal component THREE). If there was afforestation beyond 1km from the nest raven occupancy was unaffected whether it was mature or pre-thicket (principal component SIX). The amount of agricultural improvement had no detectable influence on occupancy, at least to the degree with which it occurred in the study area. Considering principal components in order (i.e. by amount of variance explained), most GULs were excluded because they lay outside the 2-dimensional convex hull formed by principal component ONE and TWO which contained 3720 non-occupied GULs. Only a further 708 of this sample could be removed because they fell outside convex hulls ONE-FIVE and TWO-FIVE. Most GULs were excluded because they were surrounded by large expanses of forestry, particularly where this was nearby. Thus there were 3012 non-occupied GULs which fell within the 3-dimensional convex hull. These GULs were therefore classed as 'suitable' for raven occupancy, based on the

variables included in the principal components analysis. Of these 421 were classed as vacant within intensive study areas; 137 with potential cliff nest-sites and 284 with only potential tree nest-sites.

Spatial distribution of results

The distribution of GULs containing mature forestry throughout the study are is shown, for reference, in Figure 8.3. Figure 8.4 shows the distribution of all GULs in the study area classed as suitable, that is lying at the centre of an area of suitable habitat for raven occupancy, and potentially containing a nest site. Many GULs in large blocks of mature plantation were unsuitable because of habitat, in addition to those in open moorland where there were unlikely to be any nest-sites (see Figure 7.5) Suitable GULs within intensive study areas which were also classed as vacant are mapped in Figure 8.5. Again, only those vacant GULs surrounded by large forest blocks were now classed as unsuitable, leaving many apparently suitable but vacant locations. This was particularly apparent on MULL where there was little forestry. Most GULs classed as vacant and which potentially contained a cliff nest-site (Figure 7.6) were subsequently classed as suitable (Figure 8.6), presumably as foresters avoid the most rugged terrain. Afforestation therefore had little impact on the suitability for occupancy of most of the vacant locations which potentially contained the preferred nest-site type.

Whilst GULs surrounded by mature plantation were unsuitable, many on the edge of plantations were still within limits suitable for occupancy. In fact, the increased availability of potential nest sites provided by mature plantation may have increased the area available for occupation, as much forest block edge was apparently suitable for occupation by ravens (Figure 8.7). Out of 3012 GULs classed as suitable, 513 (17%) contained only thicket plantation as possible nest-sites. Even in heavily afforested areas, many suitable sites occurred if mature plantation occurred in small patches and was relatively fragmented (for example COWAL).

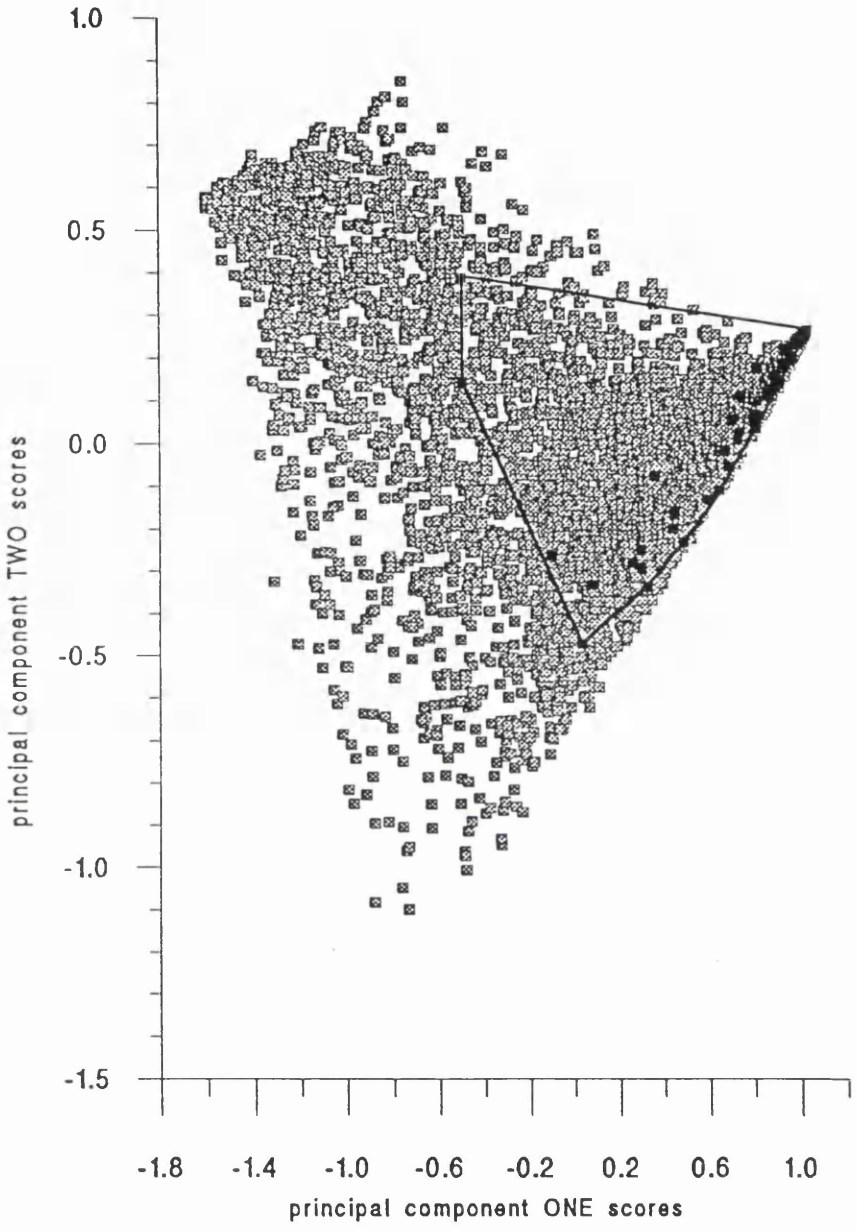

Figure 8.2 a Principal component ONE scores versus principal component TWO scores

shaded squares : GULs not containing an occupied raven site in 1990 but potentially containing a nest site
solid squares: GULs containing an occupied raven site in 1990
solid line: convex hull surrounding GULs containing an occupied raven site in 1990

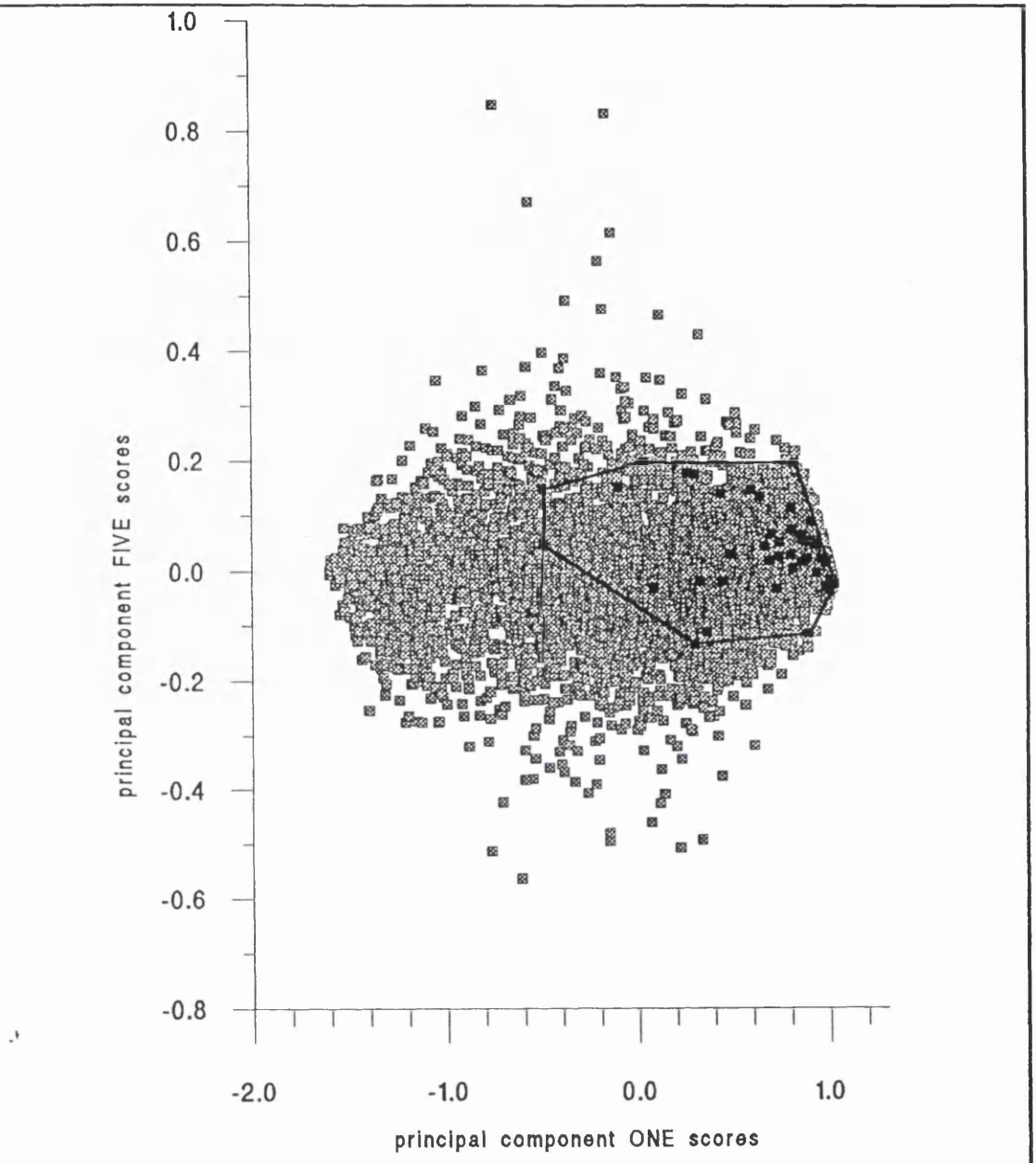

Figure 8.2 b Principal component ONE scores versus principal component FIVE scores

shaded squares : GULs not containing an occupied raven site in 1990 but potentially containing a nest site
solid squares: GULs containing an occupied raven site in 1990
solid line: convex hull surrounding GULs containing an occupied raven site in 1990

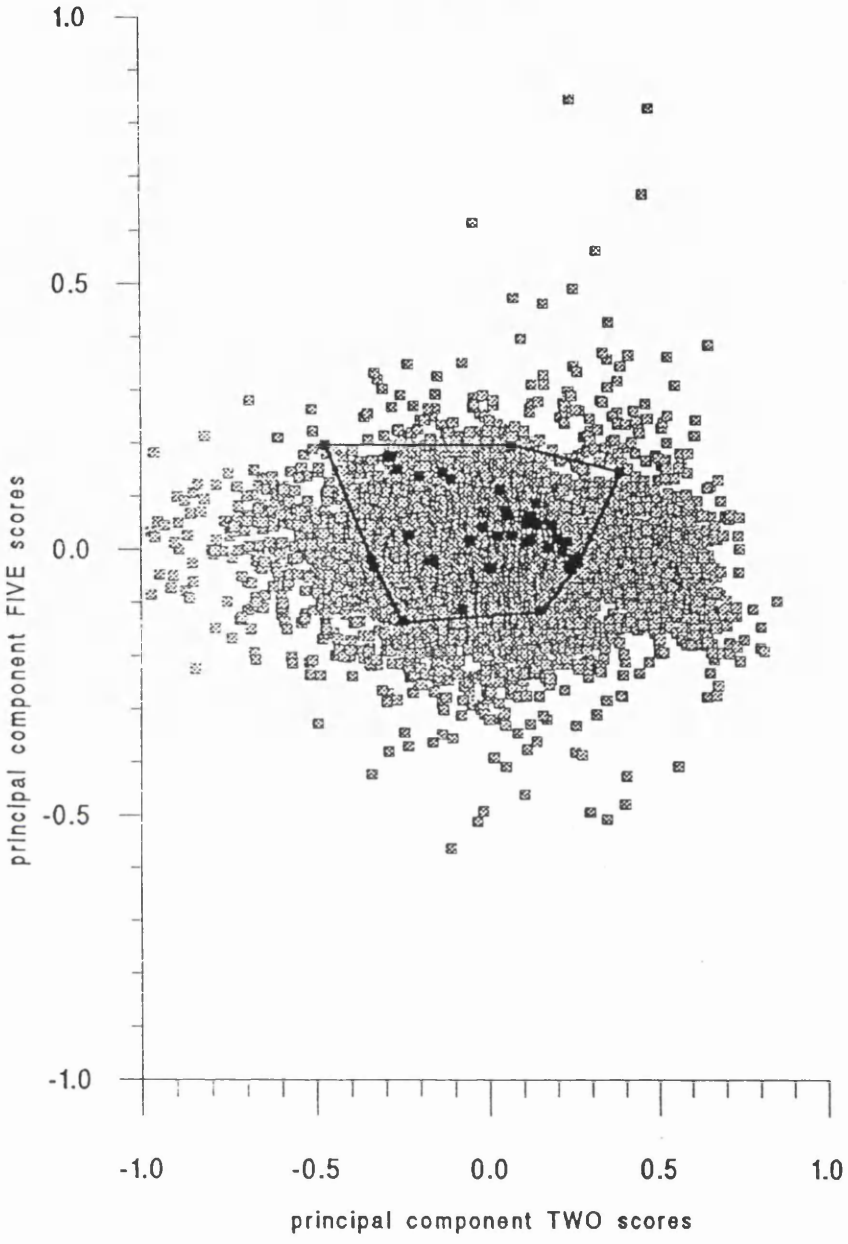

Figure 8.2 c Principal component TWO scores versus principal component FIVE scores

shaded squares : GULs not containing an occupied raven site in 1990 but potentially containing a nest site
solid squares: GULs containing an occupied raven site in 1990
solid line: convex hull surrounding GULs containing an occupied raven site in 1990

Figure 8.3 Distribution of GULs which contained mature forestry plantation.

Figure 8.4 Distribution of all GULs potentially containing a nest site and located in the centre of habitat suitable for raven occupancy.
Entire GIS study area.

Figure 8.5 Distribution of vacant GULs potentially containing a nest site and located in the centre of habitat suitable for raven occupancy.
Intensive study areas only.

Figure 8.6 Distribution of vacant GULs potentially containing a cliff nest site and located in the centre of habitat suitable for raven occupancy.
Intensive study areas only.

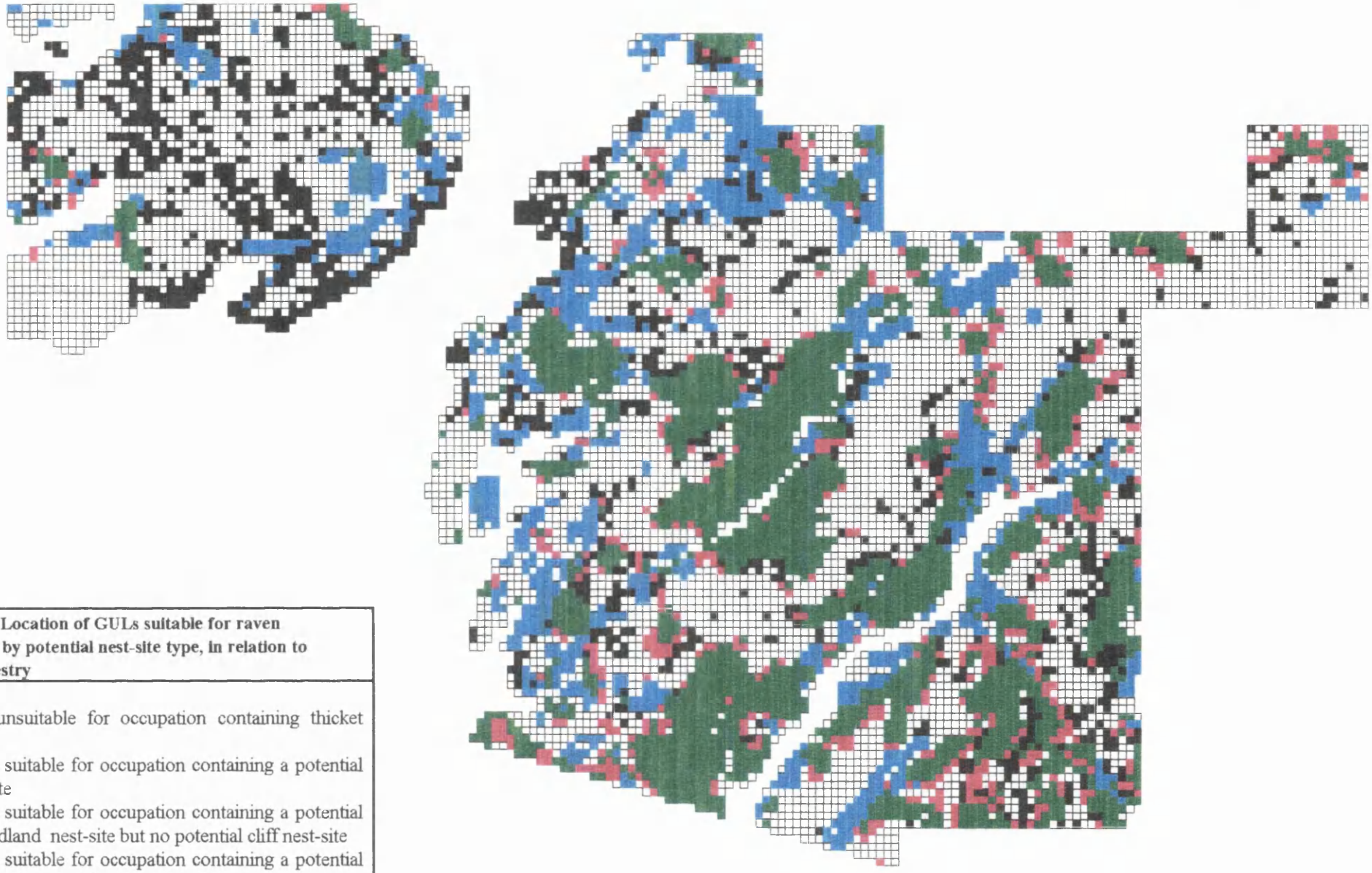

Figure 8.7. Location of GULs suitable for raven occupation by potential nest-site type, in relation to thicket forestry

KEY:

- GUL unsuitable for occupation containing thicket plantation
- GUL suitable for occupation containing a potential cliff nest-site
- GUL suitable for occupation containing a potential native woodland nest-site but no potential cliff nest-site
- GUL suitable for occupation containing a potential mature plantation conifer nest site only

PROXIMITY TO HUMAN DISTURBANCE

Ravens in the study area frequently nested next to busy roads and this was obviously no deterrent to occupancy. Ravens may, however, have been avoiding humans activity by nesting away from houses, farms and other buildings.

The distance to the nearest building from each raven nest found occupied in 1990 was calculated from GIS data by a macro in the LITES2 mapping package. A second macro was written to find the total number of buildings within a 500m radius from each of these nests.

Many raven nests were situated close to buildings: 23% of the sample were closer than 500m and 10% were closer than 250m (Figure 8.8). The buildings within 250m of occupied sites were known from fieldwork. At three nests the building(s) were working farms, and the fourth nest was located adjacent to a village. For nests which were located closer than 500m to a building (n = 9), the number of separate buildings did not appear to be important. Within this radius there was a single building at five sites, two buildings at two, three buildings at one and 10 at another. There was no relationship between the height of the nest cliff and proximity to buildings (Figure 8.9).

Ravens in mid-Argyll therefore appeared to be able to tolerate nesting close to sources of human activity. Although they may have preferred to nest as far as possible from such disturbance, they were still capable of nesting within 250m of occupied buildings. As this distance was below the resolution of the minimum unit of location (±250m) used in this study no GULs could be excluded because of proximity to buildings.

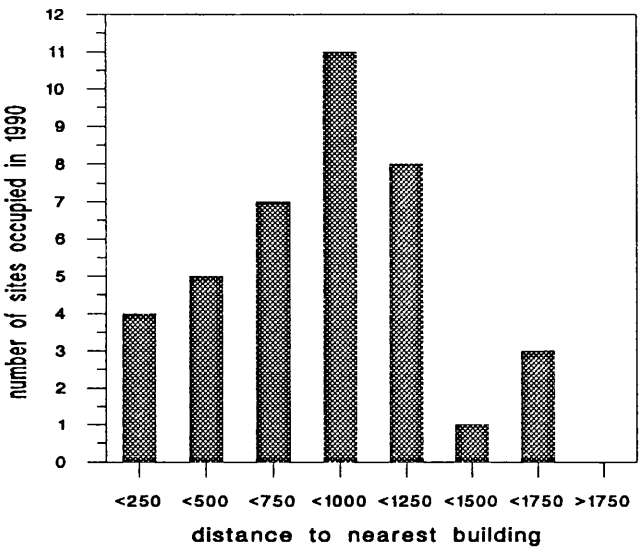

Figure 8.8. Distance from raven nests to buildings.

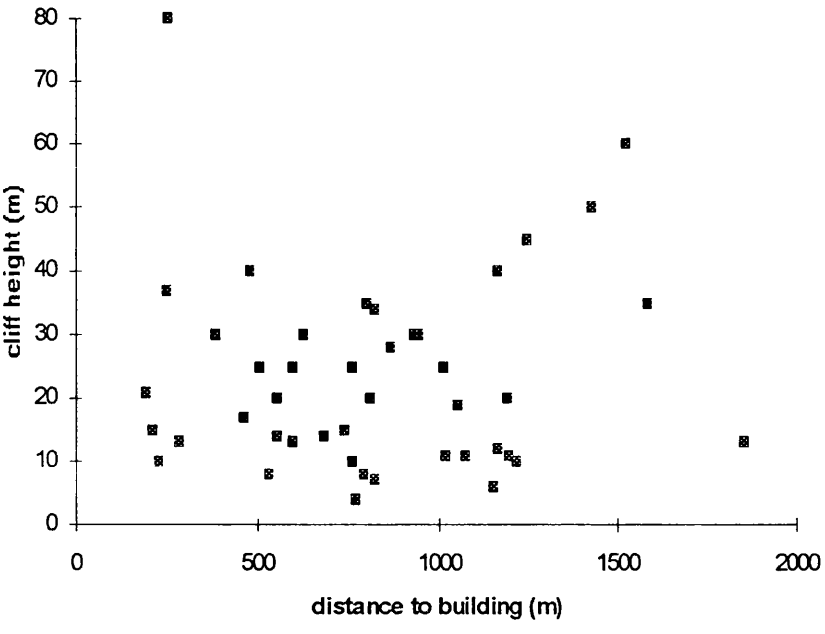

Figure 8.9. Height of nest cliff and distance to the nearest building.

TESTING PREDICTIONS

Sixty seven raven sites were known outwith intensive study areas, however many of these were located outside the area covered by the environment GIS. Nevertheless a large area did remain immediately to the south of the Lorn in which the location of many ravens were known (Figure 8.10). Predicted suitability for occupancy was mapped and overlaid with the distribution of ravens (Figure 8.11). Fifteen raven territories where nests had been found were known in this area. Of these, 13 occupied GULs that were predicted to be suitable for occupation and two were in GULs predicted to be unsuitable. Of the incorrectly classed sites, one was misclassified because the 30m tall rock face in a deep ravine, on which the actual nest was sited, was not marked on Ordinance survey maps and was consequently predicted to be unlikely to contain a potential nest-site. The second site was occupied in both 1989 and 1990, but was classified as unsuitable and was surrounded by unsuitable GULs on all sides. The nest was situated on a very tall sheer cliff and was classed as containing a potential cliff site, but was surrounded by a great deal of mature plantation and fell outside the hyper-polygon derived above. Success of the model was therefore high with 87% correctly classified.

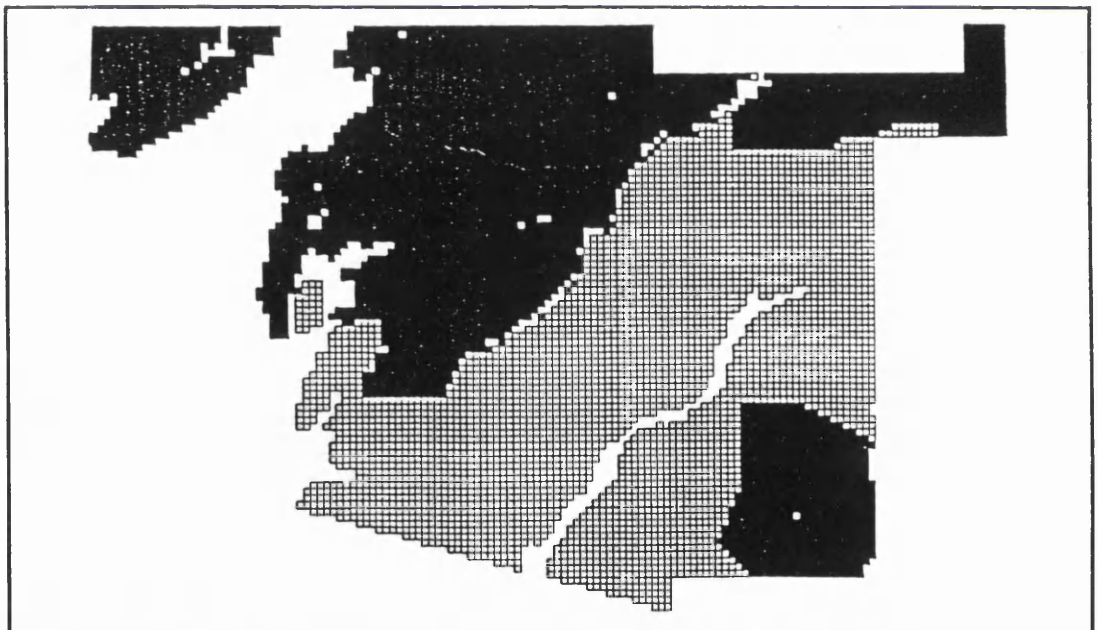

Figure 8.10 Location of test area for predictions of suitability for occupation by ravens in mid-Argyll.

■ Intensive study areas

□ Test area

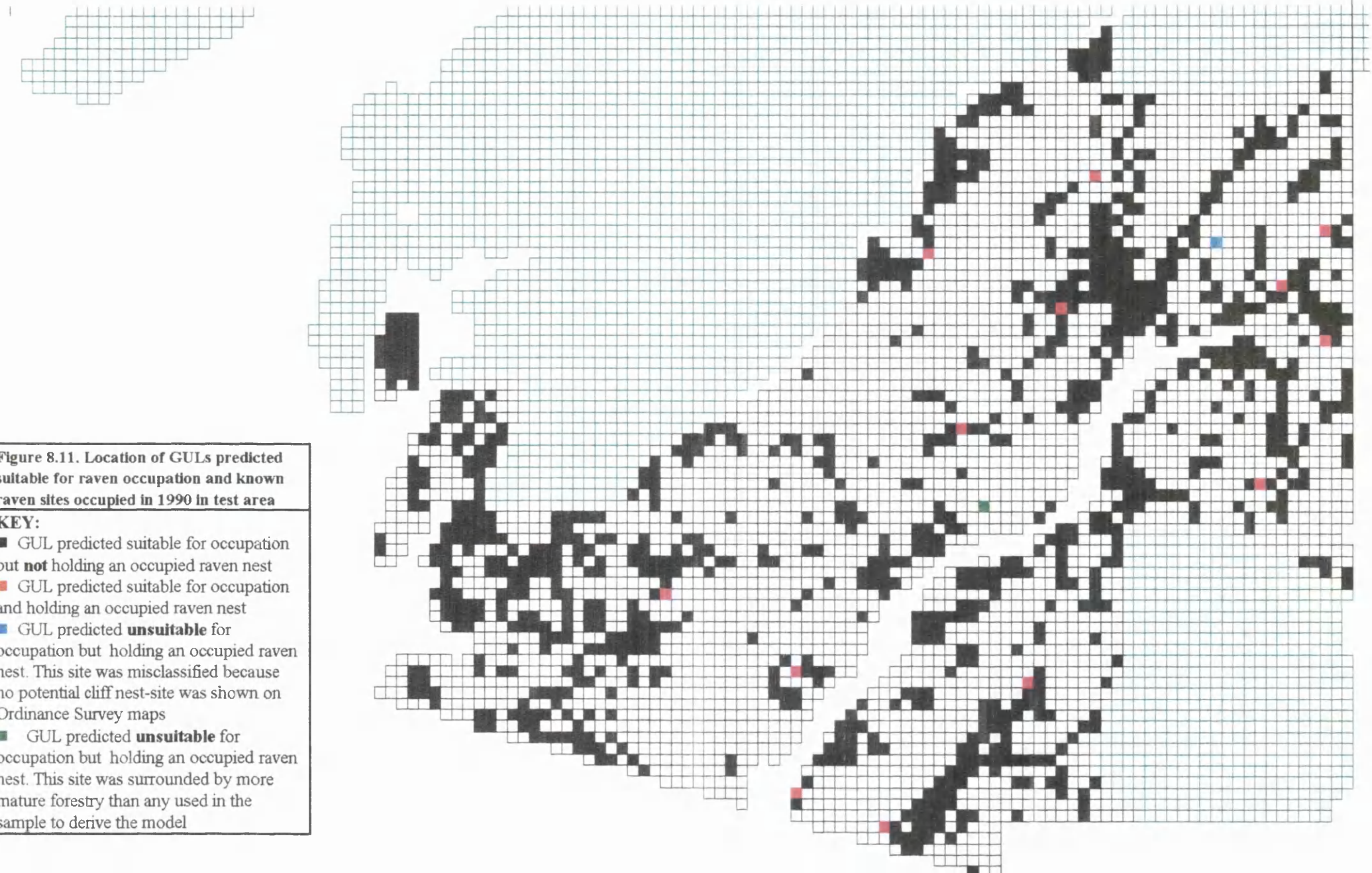

Figure 8.11. Location of GULs predicted suitable for raven occupation and known raven sites occupied in 1990 in test area

KEY:

- GUL predicted suitable for occupation but **not** holding an occupied raven nest
- GUL predicted suitable for occupation and holding an occupied raven nest
- GUL predicted **unsuitable** for occupation but holding an occupied raven nest. This site was misclassified because no potential cliff nest-site was shown on Ordinance Survey maps
- GUL predicted **unsuitable** for occupation but holding an occupied raven nest. This site was surrounded by more mature forestry than any used in the sample to derive the model

DISCUSSION

Blanket afforestation rendered land untenable for ravens in mid-Argyll. However, afforested locations were still apparently suitable for occupancy where open ground remained, for example on the edge of forest blocks. Even locations in heavily afforested areas were classed as suitable as long as the forestry was fragmented. The spatial distribution of the planting was important: the amount of afforestation in areas close to the nest, in the region of 1km and closer, was more important than the total amount of afforestation within 3km.

These findings are in broad agreement with those from the study conducted by Marquiss *et al.* (1978) in northern England and southern Scotland (reviewed in chapters 1 and 4). They found that desertion of territories was associated with afforestation (spatially and temporally) but could not find a consistent association between levels of afforestation and occupancy. They found that some pairs could withstand large amounts of forestry (up to 76% of total area in a 3km radius) whereas others were deserted at much lower levels. They attributed this to differences in the overall quality of the original habitat and the alternative food sources available, in that good habitat could support more afforestation before it became untenable than could poor habitat. In the present study the model predicted suitable locations with a range of afforestation from 0% to 62 % of land area within 3km. This may have been because those occupied sites in mid-Argyll (from which classifying limits were drawn) which contained a lot of forestry were on good habitat. Alternatively, fragmented forest may not be as detrimental to the birds as the same amount of blanket forestry.

Newton *et al.* (1982) could find no decline in occupancy of ravens with the amount of afforestation within 1km or 3km in mid-Wales. As discussed in Chapter 4, the difference between the Newton *et al.* (1982) and Marquiss *et al.* (1978) may in part have been due to differences in time-lag between habitat change and a new distribution of pairs. In addition, however, there was the difference in planting pattern between the two regions to be considered. In mid-Wales there was a much more fragmented pattern of afforestation, producing a mosaic of small plantations and open sheepwalk and farmland, whereas the majority of planting in the northern Pennines was in large blocks of 'blanket' afforestation. Newton et al. (1982) also suggested that

Welsh plantation was younger than in the northern Pennines and predicted that a change in occupancy of raven sites would occur over the next decade. A follow up study in 1986 (Cross and Davis, 1986) did not support this. Almost all forest canopy was closed by 1986 but they found no evidence that this, or any other measure of afforestation, resulted in territory desertion.

Mature afforestation provided the only potential nest sites in 17% of locations classed as suitable for occupancy. As certain levels of afforestation appeared to be tolerated, some areas previously unsuitable for ravens may have become available for occupation. I found only one pair nesting in a plantation conifer (larch *Larix* sp.) in mid-Argyll. This had no cliffs within 1km but did have large deciduous trees nearby. Cross and Davis (1986) found that tree nesting pairs in mid-Wales preferentially chose spruce (*Picea* spp.) to native trees, and that they used new nest sites in plantation, which provided sites where none had previously existed.

The 'improvement' of ground for agriculture by draining, fertilisation and reseeding, was not useful in distinguishing suitable from unsuitable ground. Newton *et al.* (1982) could detect no adverse effects of agricultural 'improvement' in mid-Wales. Again, in both areas this activity was limited in extent and tended to occur in small blocks of ground. Widespread improvement of large areas may still prove detrimental to ravens.

Sources of human disturbance did not appear to influence raven occupancy in mid-Argyll. Hooper (1977) found ravens very tolerant of human activity, whether roads or houses: one nest which was continuously occupied for many years had occupied houses 60, 90 and 150m away. Dare (1986) has noted that ravens in north Wales did not necessarily avoid humans. Knight (1984) found that ravens altered their response to human intruders when they lived in proximity to people from bold, defensive mobbing, to quiet, timid evasive actions. This response is not universal but may enable many pairs to remain undiscovered, unless deliberately tracked down, even when nesting close by (Hooper, 1977). It has been argued that ravens (and peregrines) can tolerate increased human disturbance only where tall cliffs are available as these provide a compensatory increase in protection (Ratcliffe, 1962; Holyoak and Ratcliffe, 1968). Hooper (1977) found no evidence for this in ravens in Virginia, and it was not supported by the evidence from mid-Argyll. However in both these two

regions deliberate persecution was negligible. There would, however, be a selective advantage in choosing tall cliffs, except in remote locations, for those ravens nesting in regions where persecution is a significant cause of nest failure.

The methods developed in this chapter have a broad application. They permit distinction between gaps in the distribution of an animal which can be attributed to unsuitable habitat and those which occur in suitable habitat. This latter group can then be targeted for further investigation. Using a GIS greatly facilitated overlaying of occupied and unoccupied coverages for combinations of principal components for a large number of cases. This technique may be made redundant by dynamic graphic interface systems currently being developed for statistical applications (J. Currall, pers. comm.). However, viewing the spatial distribution of statistically derived variables (e.g. maps of principal component or discriminant function scores) in the course of analyses, and overlaying these with other variables, would greatly aid interpretation in many analyses.

Further development of the approach was beyond the scope of this project, however I did consider how it could be improved in the future. The constraints for suitability could have been broadened by considering confidence limits of occupied sites in principal component space, and made more conservative by excluding outliers. An more complete solution would be to consider several convex hulls of decreasing size by incrementally removing the most outlying case (a technique known as 'peeling') and producing a 'probability' of suitability for each GUL. The analysis would also have benefited from some measure of forest fragmentation. Potentially, this could have clarified the interpretation of spatial pattern based solely on the proportion afforested in different regions and provided a better classification of suitability. Fractal analysis (Sugihara and May, 1990) would be an obvious method to determine the appropriate scale to measure forest fragmentation for ravens.

So far I have defined suitability for ravens solely by probable nest site availability and level of afforestation. Many vacant locations were apparently suitable on this basis. However, as I have discussed, the quality of

semi-natural habitats may also influence the quality of a location for ravens. This is examined in the next chapter.

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CHAPTER 9. PREDICTION OF RAVEN BREEDING PERFORMANCE

PART I. DETERMINING WHICH PARAMETERS COULD BE PREDICTED AND THE VARIABLES REQUIRED

INTRODUCTION

Raven populations from widely separated regions of Britain appeared to have the same overall reproductive success (Chapter 4). However, within each of these populations there was a range of breeding performance by individual pairs. Consistent differences in breeding performance between territories are commonly ascribed to differences in the quality of the territory or quality of the parents. These two are difficult to separate, and their separate influence may differ within a species depending upon population turnover and habitat quality (Goodburn, 1991). Whilst it may not be feasible to determine whether differences in breeding performance are due to high quality birds occupying particular habitats or the direct influence of habitat, in either case habitat will be correlated with breeding performance. Many studies have shown that breeding performance is related to the food supply available to the breeding pair (e.g. Dijkstra *et al.*, 1982; Newton, 1986; Daan *et al.*, 1989). Whilst increased production of young may be an obvious way of improving fitness, timing of breeding may also be crucial in determining the potential of the young produced to survive and subsequently breed themselves, as discussed in Chapter 1.

In the previous chapter, I identified 421 GULs in intensive study areas which were classed as potentially containing a nest site, in habitat suitable for occupancy, and also vacant; that is, outwith the territorial influence of surrounding pairs. This assessment was based upon the amount of afforestation surrounding existing pairs. These vacant sites may have differed in the quality of semi-natural habitats remaining. In this chapter I investigated whether it was possible to model aspects of breeding performance using measures of the surrounding habitat and hence predict the potential for breeding ravens at the sites listed above. Predictive modelling of breeding performance permitted an assessment of the quality of semi-natural habitats in addition to forestry without the need to resort to inference from multivariate statistics. If vacant sites of high quality for

breeding remained, then reasons other than availability of suitable habitat, at least as measured in this study, must be sought to explain the absence of ravens.

METHODS

Measures of Raven Breeding Performance

Five measures of raven breeding performance were considered for use in this analysis:

1) Whether pairs bred, yes or no

2) Whether pairs which bred were successful, yes or no

3) Clutch size

4) Fledged brood size of successful pairs

5) Laying week

Comparison of environmental variables between groups of raven territories where breeding was or was not attempted, and if so whether the attempt was successful or not, was restricted to records from 1990 as data for 1989 was considered incomplete. Measures of clutch, fledged brood and laying date were converted into binary variables. For each of these parameters, when data were available for both years the mean value was taken. The median value of each parameter for the population over both years was used to determine a cut-off value for the new binary variable. For each case the new variable was given a value of 'zero' if mean value of the relevant parameter fell below the cut-off value, and 'one' if it was equal or greater than the cut-off value. Details of sample sizes and cut-off points are given in Table 9.1.

new binary variable name	Description (class)	Cut-off value for each class		Sample size in each class	
		class 0	class 1	class 0	class 1
CLUTCH SIZE	low (0) or high (1) clutch size	<5	≥5	6	7
FLEDGE-SUCCESSFUL	Low (0) or high (1) fledged brood size of successful pairs	<3	≥3	15	18
TIMING	Early (0) or late (1) first laying week	<4.5	≥4.5	14	15

Table 9.1 Derivation of binary measures of clutch size, fledged brood size and first laying date.
The median value of each parameter for the population (1989 and 1990 combined) was used as the cut-off value for dividing the sample into two groups for each variable.

Measures of Breeding Environment.

Marquiss *et al.* (1978) found a reduction in breeding attempts, clutch and fledged brood size in response to afforestation of surrounding areas up to 5km from the nest, even though this was beyond the study area nearest neighbour distance. Ravens may forage in overlapping ranges, as indeed do many raptors (e.g. sparrowhawks, Newton, 1986, and buzzards, Tubbs, 1974). Consequently, habitat was measured in increasing areas around the nest up to a large radius of 5km.

Environmental data were extracted from the GIS in radii of increasing size for each raven site in the study area. Unlike Chapter 8, variables were measured in the full area contained within a circle rather than nested regions with increments in area. This was because each variable at each radius would be considered individually. Raster data was converted to vector format, using procedures outlined in Chapter 5, to permit measurement of boundary lengths and coverage within circular regions (raster data could be conveniently extracted only in square regions).

Landcover was measured from the classified Landsat image. As ravens were suspected to occupy large home ranges, six radii up to 5Km from the nest were considered: 0.5, 1, 2, 3, 4 and 5km. In order to take into account differences in the number of unclassified pixels on the Landsat image, areas of each class were

converted to proportion of the total number of pixels in the circle which had been classified. Converting area data in this way also standardised values from circles of different size. In addition the proportion of the land in each circle occupied by each landcover class was calculated. The distinction between proportion of the total area and proportion of land occupied by a landcover class was thought to be useful, especially as so many ravens were coastal. Original landcover classes were combined to provide more general categories of landcover such as total forestry (pre- and post-thicket), and semi-natural grassland (perennial grassland and wet heath).

Summary topographic variables were derived from the digital terrain model in the environment GIS, again from raster data converted into vector format and in radii of increasing size: 0.5, 1 and 2km. Measures of human activity were also taken in these radii. In all, 300 variables were derived for each raven site (Table 9.2).

variable type	Description of variable	Radii (Km) for which available					
		5	4	3	2	1	0.5
BUILDINGS	distance to nearest building (m)				*	*	*
	total buildings				*	*	*
	length of metalled roads				*	*	*
BOUNDARY LENGTHS	length of coastline (m)	*	*	*	*	*	*
	length of thicket stage conifer plantation boundary (m)	*	*	*	*	*	*
	length of pre-thicket stage conifer plantation boundary, excluding that abutting thicket stage conifer plantation (m)	*	*	*	*	*	*
	length of conifer plantation boundary (m)	*	*	*	*	*	*
	length of all woodland and conifer plantation boundary abutting open-land landcover classes (m)	*	*	*	*	*	*
	length of all boundaries between classes excluding those abutting fresh and salt water (m)	*	*	*	*	*	*
	length of all boundaries between all classes (m)	*	*	*	*	*	*
PROPORTION OF TOTAL AREA	pre-thicket stage conifer plantation/scrub	*	*	*	*	*	*
	thicket conifer plantation	*	*	*	*	*	*
	Calluna bog	*	*	*	*	*	*
	mixed bog	*	*	*	*	*	*
	wet heath	*	*	*	*	*	*
	improved and semi-improved grassland	*	*	*	*	*	*
	perennial grassland	*	*	*	*	*	*
	deciduous woodland	*	*	*	*	*	*
	mixed deciduous and coniferous woodland	*	*	*	*	*	*
	fresh water	*	*	*	*	*	*
	salt water	*	*	*	*	*	*
PROPORTION OF TOTAL AREA (COMBINED CATEGORIES)	total forestry: thicket + pre-thicket conifer plantation	*	*	*	*	*	*
	total mature woodland: thicket stage conifer plantation + deciduous + mixed woodland	*	*	*	*	*	*
	total bog and wet heath: *Calluna* + mixed heath + wet heath	*	*	*	*	*	*
	total bog : *Calluna* + mixed heath	*	*	*	*	*	*
	total grassland: wet heath + perennial grassland + agricultural	*	*	*	*	*	*
	total semi-natural grassland: wet heath + perennial grasslands	*	*	*	*	*	*
PROPORTION OF LAND	pre-thicket stage conifer plantation/scrub	*	*	*	*	*	*
	thicket conifer plantation	*	*	*	*	*	*
	Calluna bog	*	*	*	*	*	*
	mixed bog	*	*	*	*	*	*
	wet heath	*	*	*	*	*	*
	improved and semi-improved grassland	*	*	*	*	*	*
	perennial grassland	*	*	*	*	*	*
	deciduous woodland	*	*	*	*	*	*
	mixed deciduous and coniferous woodland	*	*	*	*	*	*

Table 9.2. Environmental variables derived from GIS data for all raven territories in the GIS study area

Variables are grouped by type, alternate shading separates types for clarity

variable type	Description of variable	Radii (Km) for which available					
		5	4	3	2	1	0.5
PROPORTION OF LAND (COMBINED CATEGORIES)	total forestry: thicket + pre-thicket conifer plantation	*	*	*	*	*	*
	total mature woodland: thicket stage conifer plantation + deciduous + mixed woodland	*	*	*	*	*	*
	total bog and wet heath: *Calluna* + mixed heath + wet heath	*	*	*	*	*	*
	total bog : *Calluna* + mixed heath	*	*	*	*	*	*
	total grassland: wet heath + perennial grassland + agricultural	*	*	*	*	*	*
	total semi-natural grassland: wet heath + perennial grasslands	*	*	*	*	*	*
TERRAIN	minimum altitude within radius				*	*	*
	maximum altitude within radius				*	*	*
	altitude range within radius				*	*	*
	modal altitude within radius				*	*	*
	median altitude within radius				*	*	*
	minimum slope within radius				*	*	*
	maximum slope within radius				*	*	*
	slope range within radius				*	*	*
	modal slope within radius				*	*	*
	median slope within radius				*	*	*
	minimum ruggedness index within radius				*	*	*
	maximum ruggedness index within radius				*	*	*
	ruggedness index range within radius				*	*	*
	modal ruggedness index within radius				*	*	*
	median ruggedness index within radius				*	*	*
	proportion of land with no aspect				*	*	*
	proportion of land in radius facing north				*	*	*
	proportion of land in radius facing east				*	*	*
	proportion of land in radius facing south				*	*	*
	proportion of land in radius facing west				*	*	*

Table 9.2. (continued) Environmental variables derived from GIS data for all raven territories in the GIS study area
Variables are grouped by type, alternate shading separates types for clarity

Univariate screening of environmental variables

As a first step in reducing this set of environmental variables down to a smaller number which were most highly influential on breeding performance, a series of univariate screenings were run against the binary measures of breeding performance. The distribution of values for environmental variables were not assumed to be normal. Comparison of the central tendency of these variables between groups was made using Mann-Whitney U-tests. Variables which showed a significant difference between any group at the 5% level were

retained for further analyses. This exercise was designed as a filter to detect variables useful for further analysis: no allowance was made for multiple comparisons and it is acknowledged that five percent of the results would be expected to be incorrect.

Predicting group membership: logistic regression analysis

The data were examined to determine their suitability for multivariate analysis. Frequency distributions of variables which differed in central tendency between groups were examined for normality using detrended normal probability plots (Tabachnick and Fidell, 1989) and univariate outliers were identified using box and whisker plots (Norušis, 1990a). Multivariate normality was assessed by examination of scatterplots of pairs of variables.

Discriminant analysis and logistic regression analysis are suitable modelling techniques to predict a binary dependent variable from a set of independent variables. However, most of the data were univariately and multivariately non-normal and there were unequal covariance matrices between groups. Discriminant analysis is sensitive to these problems (Klecka, 1980) and under such conditions logistic regression is preferred (Press and Wilson, 1978). Williams (1983), has stressed the misleading nature of results from discriminant analysis where assumptions are violated. Violation of assumptions is almost inevitable with ecological field data, and, if ignored frequently lead to erroneous interpretation of multivariate analyses (Rexstead *et al.*, 1988). Consequently some form of model validation should always be employed.

Logistic regression analysis was used to determine if a weighted linear combination of variables could be found to describe differences between groups. In a logistic model the probability of an event occurring is given by the formula:

$$p = (1+e^{-Z})^{-1}$$

where, if X_1 to X_p are independent variables, and B_1 to B_p are derived coefficients,

Z is the linear combination: $Z = \text{constant} + B_1X_1 + B_2X_2 + \ldots + B_pX_p$.

As logistic regression generates a probability of an event occurring or not which is constrained to lie between one and zero, interpretation is easier than examination of discriminant scores. In addition, this approach assumes that the probability of an event occurring is related to variables in a logistic rather than a linear manner. This approach seems more reasonable in a biological system where organisms are expected to respond to thresholds of gradients in the environment rather than a constant change over the environmental gradient (Osborne and Tigar, 1992).

In order to maintain a suitable cases to variables ratio, only small sub-sets of variables could be considered simultaneously. Sub-sets of variables for inclusion as independent variables were chosen by first considering the same variable at different radii and preferring those in which the differences in medians between groups were different at the smallest level of significance. Secondly, variables were chosen to reduce inter-correlation by examination of rank correlation matrices. Finally a preference was made for variables which would be easier to extract from the GIS for a large number of sites. It must be stressed that the object of these analyses was to calculate predictive equations rather than investigate ecological relationships. Within a logistic regression analysis both forwards and backwards stepwise selection procedures, using the likelihood-ratio statistic to select variables for removal or entry into the equation (Norušis, 1990b), were used to identify subsets of independent variables that were good predictors of the dependent variable. Interaction terms were not considered. Variables which were retained by these procedures were noted. New combinations of variables were tried on the basis of previous runs until stable and significant models were derived. Preference was given to models using the smallest number of independent variables as this reduced the time needed for extraction of information from the GIS for modelling novel sites, and the resulting model is less likely to be fine tuned to the idiosyncrasies of the data set from which it is derived and therefore more generally applicable.

Logistic models were checked using a "jackknife" approach, where each case was left out in turn from the data set used to derive the model and a comparison made between actual and predicted group membership for the excluded case.

RESULTS

Univariate screening of environmental variables against breeding performance

Environmental variables which had a significant difference in median rank between groups are given for each measure of breeding performance in Tables 9.3 - 9.8, ordered into ecologically similar groupings. Correlation matrices for these variables are given in Appendix 1. Sample sizes in tests vary due to missing values for some environmental variables, as macros written to extract data failed on a small number of cases. Visual inspection of these points was performed using the GIS and they appeared to be random with regard to habitat and so can be considered a random sample of omissions. The causes of these failures were difficult to diagnose and would have required an inordinate amount of time to correct.

Territories where pairs bred in 1990 had significantly less broad leafed woodland in a radius of 500m around the nest than territories where no breeding attempt was made (Table 9.3). This may have reflected nest-site preferences of ravens (see Chapter 7) as cliff sites are preferred to trees. No other environmental variables were found to significantly differ between these groups.

Differences in surrounding habitat between pairs which were successful and those which were unsuccessful in 1990 were significant for many variables (Table 9.4). These were grouped into seven broad categories: sea, fresh water, forestry, bog, grassland, boundary lengths, terrain, and human disturbance. Within each category, different measures or radii were always consistent in the direction of difference between unsuccessful or successful pairs. Successful pairs had more coast at a 5000m radius than failed pairs, but differences at smaller radii were not significant. Failed pairs had more fresh water within all radii from 1000m to 5000m. In general landcover categories were different between groups only at larger radii, of 3000-5000m perhaps reflecting the home range size of the birds. Failed pairs had more total forestry in this range whether recorded as proportion of the total area or as proportion of land. These relationships appeared to be due solely to the amount of mature plantation cover as differences were significant when this was considered separately, but there were no differences between groups in the amount of pre-thicket plantation. Successful pairs also had less *Calluna* bog in radii from 1000-5000m, and more grassland at large radii, with the exception of perennial

grassland within 1000m. There were more roads around successful nests and a variety of measurements of boundary lengths were consistently longer for failed pairs than successful ones: again, these probably reflected elevation as there were more roads, and greater habitat diversity and fragmentation in valley floors and towards the coast.

Significant differences in surrounding habitat between pairs producing small or large clutches were, with the exception of one terrain variable, exclusively concerned with afforestation within areas from 1000-5000m radius (Table 9.5). The direction of differences were consistent: pairs producing low clutches had more forestry, both mature and pre-thicket, than pairs producing large clutches. In addition, pairs with low clutch size had less flat ground within a 1000m radius.

Fledged brood size did not appear to be influenced by habitat, as no landcover categories were significantly different between groups (Table 9.6). However, nests producing larger broods came from areas with high topographic diversity as indicated by higher values for minimum slope and ruggedness within 500m of the nest.

Differences in surrounding habitat between pairs breeding early or late in the season were significant for many variables (Table 9.7). Again, when grouped into broad categories, the direction of differences were consistent. Landcover variables tended to be significant only at radii from 3000-5000m, whereas terrain measures (including sea) were different at radii from 1000-5000m. Early nesting was associated with lower altitudes and closer to the coast (sea and terrain variables were highly inter-correlated). Early pairs had less bog and grassland surrounding them than late nesters. Again this was probably due to inter-correlation with altitude and coast. There was a strong negative correlation between grassland and bog with measures of sea coast and positive correlation for both these land covers with altitude. Native woodland also occurred mainly at lower elevations; there was more surrounding early nesters than late nesters. Similarly there were more buildings at lower elevations.

variable subject	Variable	radius	p	n	not breeding vs. breeding attempted
native woodland	deciduous woodland (proportion of radius)	500	0.037	57	>
	deciduous woodland (proportion of land)	500	0.041	57	>

Table 9.3 Habitat variables with significantly different medians between territories where breeding was or was not attempted

variable subject	variable	radius	p	n	failed vs. successful
sea	length of coastline	5000	0.036	37	<
	salt water (proportion of radius)	5000	0.022	35	<
fresh water	fresh water (proportion of radius)	1000	0.005	34	>
	"	2000	0.020	35	>
	"	3000	0.030	33	>
	"	4000	0.019	37	>
	"	5000	0.025	35	>
forestry	total forestry (proportion of land)	4000	0.029	37	>
	"	5000	0.043	35	>
	total forestry (proportion of radius)	4000	0.024	37	>
	"	5000	0.025	35	>
	thicket conifer (proportion of radius)	3000	0.050	33	>
	"	4000	0.024	37	>
	"	5000	0.020	35	>
	thicket conifer (proportion of land)	3000	0.042	33	>
	"	4000	0.032	37	>
	"	5000	0.024	35	>

Table 9.4 Habitat variables with significantly different medians between territories where breeding attempts were successful or failed.

Continued on next page

variable subject	variable	radius	p	n	failed vs. successful
bog	Calluna bog(proportion of radius)	1000	0.034	34	>
	"	2000	0.014	35	>
	"	3000	0.016	33	>
	"	4000	0.018	37	>
	"	5000	0.004	35	>
	Calluna bog (proportion of land)	2000	0.022	35	>
	"	3000	0.020	33	>
	"	4000	0.028	37	>
	"	5000	0.009	35	>
grassland	total grassland (proportion of land)	5000	0.036	35	<
	total semi-natural grassland (proportion of land)	4000	0.045	37	<
	"	5000	0.030	35	<
	perennial grassland (proportion of radius)	1000	0.041	34	>
variable subject	**variable**	**radius**	**p**	**n**	**failed vs. successful**
ecotones	length of all boundaries between all classes	4000	0.041	37	>
	"	3000	0.025	37	>
	"	2000	0.038	37	>
	"	1000	0.044	37	>
	length of boundary between all terrestrial classes	5000	0.041	37	>
	"	3000	0.035	37	>
	"	2000	0.038	37	>
	"	1000	0.048	37	>
	length of all woodland and conifer plantation boundary abutting open land	4000	0.044	37	>
	length of pre-thicket conifer abutting non-forestry	4000	0.049	37	>
terrain	modal altitude within radius-	1000	0.012	34	>
	"	0500	0.048	37	>
human	total length of metalled roads in radius	0500	0.046	37	<

Table 9.4 (continued) Habitat variables with significantly different medians between territories where breeding attempts were successful or failed.

variable subject	Variable	radius	p	n	Group small vs. large
forestry	total forestry (proportion of land)	1000	0.031	13	>
	total forestry (proportion of radius)	1000	0.031	13	>
	thicket conifer (proportion of radius)	1000	0.040	13	>
	thicket conifer (proportion of land)	1000	0.040	13	>
	pre-thicket conifer plantation (proportion of radius)	4000	0.022	13	>
	"	5000	0.046	13	>
	pre-thicket conifer plantation (proportion of land)	5000	0.032	13	>
ecotones	length of conifer plantation boundary	4000	0.022	13	>
	"	1000	0.044	13	>
	length of thicket conifer plantation boundary	4000	0.046	13	>
terrain	proportion of land with no aspect	1000	0.044	13	<

Table 9.5 Habitat variables with significantly different medians between territories with small or large clutch size

variable subject	Variable	radius	p	n	Group small vs. large
terrain	minimum slope within radius	500	0.010	33	<
	minimum ruggedness index within radius	500	0.025	33	<
	proportion of land facing east	500	0.042	33	<

Table 9.6 Habitat variables with significantly different medians between territories with small or large fledged brood size

variable subject	variable	radius	p	n	early vs. late
sea	Salt Water (Proportion Of Radius)	1000	0.012	27	>
	"	2000	0.002	29	>
	"	3000	0.001	26	>
	"	4000	0.001	27	>
	"	5000	0.029	28	>
	length of coastline in radius	1000	0.040	29	>
	"	2000	0.006	29	>
	"	3000	0.008	29	>
	"	4000	0.013	29	>
	"	5000	0.027	29	>
bog	total bog (proportion of radius)	3000	0.023	26	<
	"	4000	0.002	27	<
	"	5000	0.035	28	<
	total bog and wet heath (proportion in radius)	3000	0.038	26	<
	"	4000	0.012	27	<
	Calluna bog (proportion of radius)	2000	0.036	29	<
	"	3000	0.035	26	<
	"	4000	0.035	27	<
	mixed bog (proportion of radius)	4000	0.033	27	<
grassland	total grassland (proportion in radius)	2000	0.013	27	<
	"	3000	0.001	26	<
	"	4000	0.003	27	<
	"	5000	0.043	28	<
	total semi-natural grasslands (proportion in radius)	2000	0.010	27	<
	"	3000	0.001	26	<
	"	4000	0.001	27	<
	"	5000	0.039	28	<

Table 9.7 Habitat variables with significantly different medians between pairs which laid early or late in the season.

variable subject	variable	radius	p	n	early vs. late
native woodland	deciduous woodland (proportion of land)-	2000	0.020	29	>
	"	3000	0.010	26	>
	"	4000	0.004	27	>
ecotones	length of boundary between all terrestrial classes	3000	0.045	29	<
terrain	maximum altitude within radius	0500	0.018	29	<
	"	1000	0.008	27	<
	"	2000	0.001	26	<
	maximum slope within radius	2000	0.025	26	<
	median altitude within radius	0500	0.029	29	<
	"	1000	0.011	27	<
	"	2000	0.038	26	<
	median slope within radius	0500	0.031	29	<
	"	1000	0.020	27	<
	"	2000	0.002	26	<
	modal altitude within radius-	0500	0.024	29	<
	"	2000	0.038	26	<
	modal slope within radius	1000	0.007	27	<
	"	2000	0.006	26	<
	proportion of land facing north	0500	0.018	29	<
	"	1000	0.009	27	<
	altitude range within radius	0500	0.027	29	<
	"	1000	0.005	27	<
	"	2000	0.001	26	<
	slope range within radius	2000	0.027	26	<
	length of river within radius	1000	0.035	29	<
human	number of buildings in radius	500	0.045	26	>

Table 9.7 (continued) Habitat variables with significantly different medians between pairs which laid early or late in the season.

Logistic regression analysis

Variables which differed between groups at the 5% level of significance were considered for inclusion in the logistic regression analysis. Although it is not necessary for variables to differ significantly between groups to justify their inclusion on theoretical grounds, choosing this level provided a useful filter to reduce an otherwise unmanageable number of potential variables to a manageable number. Also variables differing between groups only at higher levels of significance will rarely, in practice, be retained by the analysis.

Breeding attempt

Breeding was attempted at 42 sites in the sample and not attempted at 15. To reduce the discrepancy in sample size of these two groups to within acceptable limits, the first group was reduced to 30 randomly sampled cases. Only two variables were available for inclusion in the model: deciduous woodland in a 500m radius as a proportion of all classified pixels, or of classified land pixels. A significant logistic model was produced which used the former variable and a constant (Table 9.8), however this performed very poorly in re-classification (Table 9.9). Clearly, it was not possible to predict whether breeding would be attempted or not on the basis of the variables considered in this analysis.

Variable (X)	Estimated coefficients (B)
deciduous woodland (proportion of 500m radius)	-3.1735
constant	0.9267
Deviance	55.04
df	43
Sig.	0.24

Table 9.8 Logistic model of breeding attempt and environment

		Predicted		% Correct
		NON-BREED	BREED	
Observed	NON-BREED	2	13	13.33
	BREED	1	29	96.67
Total				68.89

Table 9.9 Re-classification table for loglinear model of environment and breeding attempt.
cut-off probability of classification into class 'BREED' set at p = 0.5

Success

There were 53 habitat variables which differed significantly between successful and unsuccessful breeding attempts, and these fell into eight categories. However, even though a great many sub-sets of variables were tried, all converged on a model which used one variable only: modal altitude within a radius of 1000m, plus a constant (Table 9.10). This model was the most successful at re-classification, but was unable to correctly predict failure (Table 9.11). It was not possible to predict the success of a breeding attempt using the variables considered.

Variable (X)	Estimated coefficients (B)
modal altitude within 1000m radius	-0.0110
constant	2.2933
Deviance	36.327
df	32
Sig.	0.274

Table 9.10 Logistic model of breeding success and environment

		Predicted		% Correct
		FAILED	SUCCESS	
Observed	FAILED	4	7	36.36
	SUCCESS	2	21	91.30
Total				75.53

Table 9.11 Re-classification table for loglinear model of environment and success.
cut-off probability of classification into class 'SUCCESS' set at p = 0.5

Clutch size

As there were few cases from which to construct a model only two variables could be entered simultaneously. However significant models were produced which included one or two forestry variables only. The best of these used only the amount of thicket conifer plantation within 1000m (Table 9.12). Using this model, the

probability of having a low or high clutch size was correctly re-classified in 11 out of 13 cases when all cases were included in the model (Table 9.13), and remained as good at predicting cases left out of the model (Table 9.14). It was possible, therefore, to predict high or low clutch size to reasonable precision using area data only.

Variable (X)	Estimated coefficients (B)
thicket conifer plantation within 1000m radius (proportion of radius)	-116.527
constant	1.3257
Deviance	10.595
df	11
Sig.	0.4778

Table 9.12 Logistic model of clutch size and environment

		Predicted		% Correct
		SMALL	LARGE	
Observed	SMALL	4	2	66.67
	LARGE	0	7	100.00
Total				84.62

Table 9.13 Re-classification table for loglinear model of environment and clutch size.
cut-off probability of classification into class 'LARGE' set at p = 0.5

		Predicted		% Correct
		SMALL	LARGE	
Observed	SMALL	4	2	66.67
	LARGE	0	7	100.00
Total				84.62

Table 9.14 Jackknifed classification of loglinear model of environment and clutch size..
cut-off probability of classification into class 'LARGE' set at p = 0.5

Fledged brood size

As there were only three variables for inclusion in modelling all could be entered simultaneously. Backwards stepwise logistic regression produced a significant model which included only the minimum slope within a 500m radius of the nest (Table 9.15), however this performed very poorly at re-classification (Table 9.16). It was not possible to predict high or low fledged brood size using the variables considered.

Variable (X)	Estimated coefficients (B)
minimum slope within 500m radius	0.3785
constant	-0.8468
Deviance	38.43
df	31
Sig.	0.1684

Table 9.15 Logistic model of fledged brood size and environment

		Predicted		% Correct
		SMALL	LARGE	
Observed	SMALL	7	8	46.67
	LARGE	2	16	88.89
Total				69.70

Table 9.16 Re-classification table for loglinear model of environment and fledged brood size.
cut-off probability of classification into class 'LARGE' set at p = 0.5

Timing of breeding

Models converged on formulations involving measures of altitude, grasslands and sea. Many models resulted in high classification rates and preference was given to models which used variables that would minimise effort required for extraction of data for novel sites from the GIS. The best of these models (Table 9.17)

correctly re-classified 96.2% of cases overall, with an optimum cut-off level of 0.4 (Table 9.18). A jackknifed classification, with cut-off level set to 0.4, correctly classified 88.5% of cases (Table 9.19). It was therefore possible to predict early or late breeding using area data only.

Variable (X)	Estimated coefficients (B)
maximum altitude within1000m radius	+0.03
proportion of semi-natural grassland within 3000m radius	+51.57
proportion of sea within 3000m radius	+7.64
constant	-25.63
Deviance	11.62
df	22
Sig.	0.965

Table 9.17 Logistic model of timing of breeding and environment

		Predicted		% Correct
		EARLY	LATE	
Observed	EARLY	12	1	92.31
	LATE	0	13	100.00
Total				96.15

Table 9.18 Reclassification table for loglinear model of environment and timing of breeding.
cut-off probability of classification into class 'LATE' set at p = 0.4

		Predicted		% Correct
		EARLY	LATE	
Observed	EARLY	11	2	84.62
	LATE	1	12	94.31
Total				88.46

Table 9.19 Jackknifed classification of loglinear model of environment and timing of breeding..
cut-off probability of classification into class 'LATE' set at p = 0.4

Thus, in summary, it was not possible to predict whether or not breeding would be attempted, and predictions of success were unreliable. Clutch size predictions were good: no sites where clutch size were predicted to be small actually produced large clutches, and only a few sites predicted to produce large clutches actually produced small clutches. Fledged brood size could not be predicted except sites expected to hold small broods generally did so. Predictions of laying week were extremely good.

PART II. MAKING PREDICTIONS FOR THE ENTIRE STUDY AREA.

INTRODUCTION

The previous section showed that predictions could be made for high or low clutch size and early or late breeding. For both models only area data needed to be considered, rather than boundary lengths. This was fortunate as the computer time needed to extract vector data for the number of GULs still in the analysis at this point was prohibitive (I estimated programs would run for four months!). Instead raster data was used to compute the same variables in a much shorter period. However, this is only convenient when extracted in square regions around points rather than the circles used in part 1. In addition, squares were centred on the centre of GULs rather than raven nests and therefore data for a raven site could have been displaced by up to 250m. Consequently, it was unlikely that regression equations derived in part I would still produce good results with the new data set. Consequently I extracted a reduced set of variables (based on those found useful in part1) from the environment GIS using macros written to use raster format data, and repeated the analysis from univariate screening onwards.

METHODS

Raster variables considered

Using a macro, pixel counts were made in square regions surrounding GULs using the landcover and altitude raster maps in the environment GIS. From these counts 75 variables were computed, within a range of squares with side lengths from 500m to 10km (Table 9.20). Variables were calculated as the proportion of all classified pixels in the region, and calculation of proportion of land was dropped as this did not appear to add useful information.

variable type	Description of variable	length of side of square (km) for which available					
		10	8	6	2	1	0.5
PROPORTION OF TOTAL AREA	pre-thicket stage conifer plantation/scrub	*	*	*	*	*	*
	post-thicket conifer plantation	*	*	*	*	*	*
	Calluna bog	*	*	*	*	*	*
	mixed bog	*	*	*	*	*	*
	wet heath	*	*	*	*	*	*
	improved and semi-improved grassland	*	*	*	*	*	*
	perennial grassland	*	*	*	*	*	*
	fresh water	*	*	*	*	*	*
	salt water	*	*	*	*	*	*
PROPORTION OF TOTAL AREA (COMBINED CATEGORIES)	total forestry: post- + pre-thicket conifer plantation	*	*	*	*	*	*
	total bog : *Calluna* + mixed heath	*	*	*	*	*	*
	total grassland: wet heath + perennial grassland + agricultural	*	*	*	*	*	*
TERRAIN	maximum altitude within radius				*	*	*

Table 9.20. Variables used in deriving logistic models from raster data

Univariate screening and production of logistic regression models

Clutch size

The logistic regression in part 1 required only measurement of mature forestry within a 1km radius. Consequently only small squares with side lengths from 250m to 2.5km were considered when examining differences between habitat in regions around nests with large clutches and small clutches. Only one variable was found to differ significantly between these two groups: pairs with smaller clutches had more mature forestry within a 1km square around the nest (Table 9.21).

variable subject	Variable (proportion of total classified pixels in square)	side of square (km)	p	n	small clutch vs. large clutch
forestry	thicket conifer plantation	1	0.014	13	S > L

Table 9.21 Habitat variables (raster data) with significantly different medians between territories where clutch size was small or large

A significant logistic regression model was derived using this variable (Table 9.22), which performed well at re-classification of cases included in the model (Table 9.23) and in correctly classifying cases which were left out of each model during jackknifing (Table 9.24). The classification tables are identical to those produced in part 1 using vector data, and clearly there was no adverse affect of modelling with pixel count data extracted in square regions around GULs.

Variable (X)	Estimated coefficients (B)
post-thicket conifer plantation (proportion of 1000m square)	-1054.40
constant	1.2528
Deviance	9.535
df	11
Sig.	0.57

Table 9.22 Logistic model of clutch size and post-thicket conifer within a 1km square (raster data).

		Predicted		% Correct
		SMALL	LARGE	
Observed	SMALL	4	2	66.67
	LARGE	0	7	100.00
Total				84.62

Table 9.23 Re-classification table for loglinear model of clutch size and thicket conifer within a 1km square clutch size (raster data).
cut-off probability of classification into class 'LARGE' set at p = 0.5

		Predicted		% Correct
		SMALL	LARGE	
Observed	SMALL	4	2	66.67
	LARGE	0	7	100.00
Total				84.62

Table 9.24 Jackknifed classification table for loglinear model of clutch size and thicket conifer within a 1km square clutch size (raster data).
cut-off probability of classification into class 'LARGE' set at p = 0.5

Timing of breeding

The logistic regression in part 1 required measurement of several variables in small and large radii. Consequently, information from squares of all sizes collected were considered when examining differences between habitat in regions around early pairs and late pairs. Differences were significant for seven variables

(Table 9.25). Early breeders had more sea within a 6km sided square and lower maximum altitude values for the range of areas considered. Landcover variables which differed between groups were bog and perennial grassland in 500m sided squares and total grassland in 6km sided squares.

variable subject	Variable (proportion of total classified pixels in square)	side of square (km)	p	n	Group early vs. late
landcover	bog	0.5	0.034	28	E < L
	perennial grassland	0.5	0.035	28	E < L
	total grassland	6	0.014	26	E < L
terrain	sea	6	0.038	26	E > L
	maximum altitude	0.5	0.018	28	E < L
	maximum altitude	1	0.017	28	E < L
	maximum altitude	2	0.013	27	E < L

Table 9.25 Habitat variables (raster data) with significantly different medians between territories where breeding was early or late

All subsets of variables were entered into logistic regressions. The best of these produced a significant logistic regression model using perennial grassland in 500m sided squares and the total grassland in 6km sided squares (Table 9.26). This model performed well at re-classification of cases included in the model with 85% correct at a cut-off level of p>0.05 for membership of the 'late' group. This was improved to 88% by setting the cut-off level to p > 0.053 (Table 9.27). The model was robust as it correctly classified 83% of cases during jackknifing, using an optimum cut-off level of p>0.056 for membership of the 'late' group (Table 9.28). The classification success obtained when jackknifing was lower than that obtained in part I using vector data, but was still adequate, and the small reduction did not justify the considerable effort required to extract vector data from the GIS.

Variable (X)	Estimated coefficients (B)
perennial grassland (proportion of 500m side square)	183.68
total grassland (proportion of 6km side square)	8.95
constant	-3.08
Deviance	25.26
df	23
Sig.	0.34

Table 9.26 Logistic model of timing of breeding using raster data.

		Predicted		% Correct
		EARLY	LATE	
Observed	EARLY	14	0	100.00
	LATE	3	9	75.00
Total				88.46

Table 9.27 Re-classification table for loglinear model of timing of breeding using raster data.
cut-off probability of classification into class 'LATE' set at $p > 0.53$

		Predicted		% Correct
		EARLY	LATE	
Observed	EARLY	14	0	100.00
	LATE	4	8	66.67
Total				83.33

Table 9.28 Jackknifed classification table for loglinear model of timing of breeding using raster data.
cut-off probability of classification into class 'LATE' set at $p > 0.56$

METHODS TO PREDICT CLUTCH SIZE AND TIMING OF BREEDING FOR VACANT GULS.

In previous chapters I identified 421 GULs in intensive study areas which were classed as containing a potential nest-site (chapter 7), in habitat suitable for occupancy (chapter 8), and vacant, that is outwith the territorial influence of surrounding pairs (chapter 6). Of these, 137 contained potential cliff nest sites, whilst 284 contained only potential tree nest sites. Predicted class of clutch size (large or small) and timing of breeding (early or late) were calculated from logistic regression equations derived above for 407 of these sites (Table 9.29). As with vector data extraction, macros written to extract data failed for a small number of cases ($^{14}/_{421}$ cases =3%) which appeared to be random with regard to habitat and so can be considered a random sample of omissions. Again, the causes of these failures were difficult to diagnose and would have required an inordinate amount of time to correct.

RESULTS

Predicted clutch size, timing of breeding in relation to potential nest-site type

60% of vacant GULs were predicted to be suitable for the production of large clutches and 31% for early breeding. 55 vacant GULs (14%) were predicted to be suitable for both (Table 9.29). These GULs were not

restricted to less preferred potential nest-site types: when only vacant GULs which contained potential cliff nest-sites were considered, 15% (5% of all vacant GULs) were predicted to be suitable for early laying of large clutches (Table 9.30). When GULs containing potential native woodland nest-sites, but no cliffs, were considered (Table 9.31), a similar figure of 18% was predicted to be both early and support large clutches. However, sites which contained potential nest-sites only in thicket forestry were predicted to be of lower quality for production of eggs as only 1.4% were predicted to support large clutches. The proportion predicted to lay early did not differ markedly with the type of nest sites potentially available (Table 9.32).

all potential nest site types	EARLY LAYING	LATE LAYING	clutch total
LARGE CLUTCH	55	188	243
SMALL CLUTCH	72	92	164
timing total	127	280	
		total	407

Table 9.29 Predicted clutch size and timing of breeding of vacant GULs, suitable for occupancy and potentially containing a nest site.

potential cliff nest sites	EARLY LAYING	LATE LAYING	clutch total
LARGE CLUTCH	20	93	113
SMALL CLUTCH	14	9	23
timing total	34	102	
		total	136

Table 9.30 Predicted clutch size and timing of breeding of vacant GULs, suitable for occupancy and potentially containing a cliff nest site.

potential native tree nest sites	EARLY LAYING	LATE LAYING	clutch total
LARGE CLUTCH	35	94	129
SMALL CLUTCH	31	39	70
timing total	66	133	
		total	199

Table 9.31 Predicted clutch size and timing of breeding of vacant GULs, suitable for occupancy and potentially containing a nest site in native woodland.
Excluding those GULs which also contained potential cliff sites

	EARLY LAYING	LATE LAYING	clutch total
LARGE CLUTCH	0	1	1
SMALL CLUTCH	27	44	71
timing total	27	45	
		total	72

Table 9.32 Predicted clutch size and timing of breeding of vacant GULs, suitable for occupancy and potentially containing a nest site in mature plantation forestry.
Excluding those GULs which also contained potential cliff sites or native woodland nest sites

Spatial distribution of results

The distribution of predicted timing of breeding and clutch size for all GULs classed as vacant (Chapter 6), containing a potential nest-site (Chapter 7), and in habitat suitable for occupancy (Chapter 8) is shown in Figure 9.1. I estimated the maximum number of raven territories that could have been fit into areas classed as vacant by fitting as many solid disks of radius 0.5 x overall mean NND (1.7Km, at the same scale as maps) into these areas, starting first by 'occupying' those GULs predicted to support early laying of large clutches. Estimates of the number of unclaimed territories (missing pairs) are given in Table 9.33. There were many

locations in all study areas which were apparently suitable for ravens and which also were predicted to be suitable for early laying of large clutches These were not restricted to sites containing only less preferred nest-site types as there were still many pairs missing when only GULs which contained potential cliff sites were considered (Table 9.34, Figure 9.2). These may be expected to be the most preferred sites, and the first to be occupied by new recruits.

intensive study area	estimated number of pairs which could be situated in suitable[1] GULs with predicted early laying of large clutches	estimated number of pairs which could be situated in suitable[1] GULs predicted to be either late laying, small clutches , or both	estimated total number of pairs which could be located in vacant GULs (unclaimed territories)	number of occupied territories in 1990	% unclaimed territories [2]
Lorn	10	17	27	26	51
Cowal	1	4	5	7	42
Mull	6	9	15	17	47
Glens	0	10	10	2	83
Total	17	40	57	52	52

Table 9.33. Estimated number of unclaimed territories from intensive study areas: all potential nest-site types

[1] suitable GULs were those classed as vacant (Chapter 6), containing a potential nest-site (Chapter 7), in habitat suitable for occupancy (Chapter 8), and graded according to suitability for production of large clutches and early laying (this Chapter).

[2] $= \left({}^{\text{unclaimed territories}} / {}_{\text{(unclaimed territories + occupied territories)}} \right)$

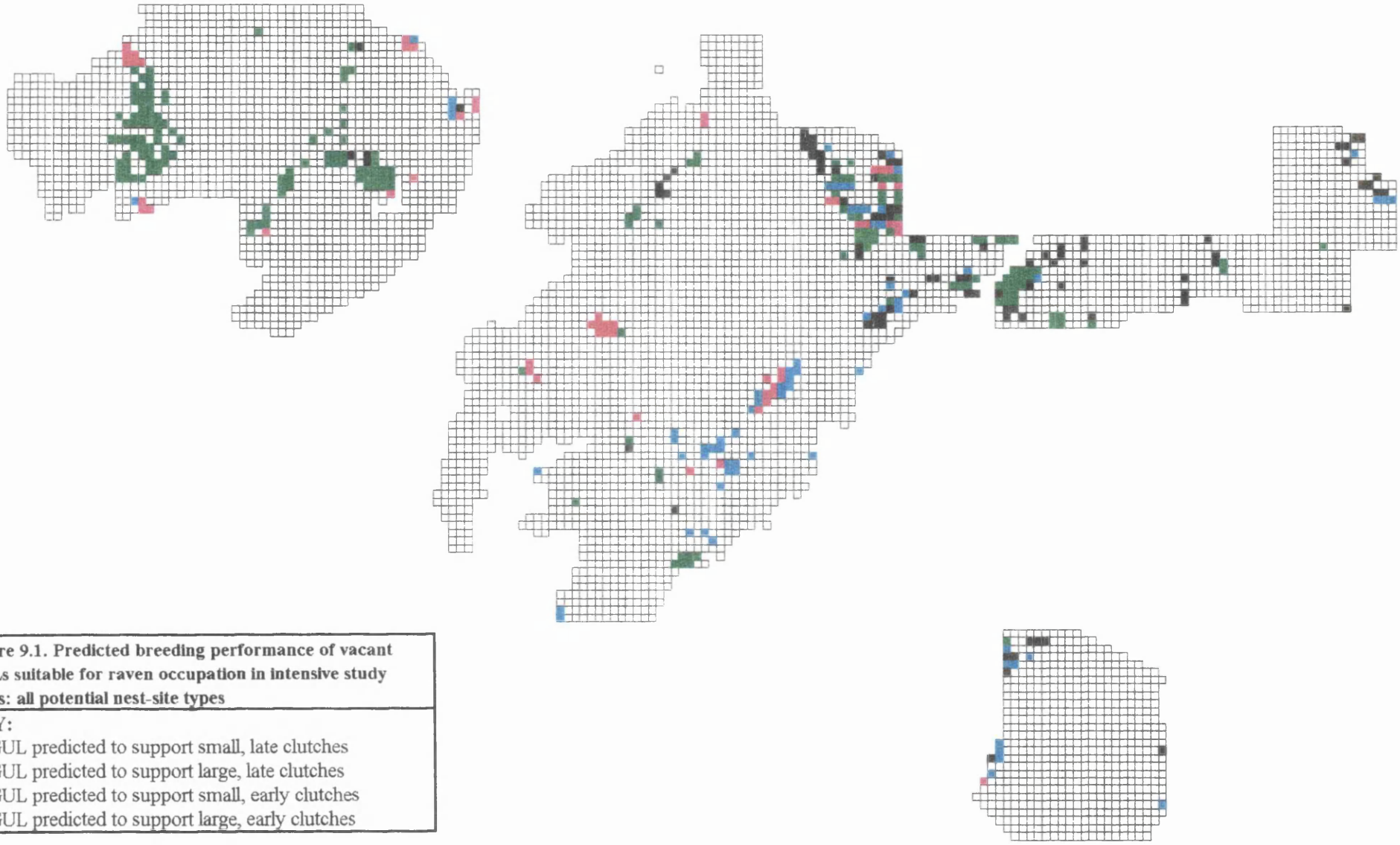

Figure 9.1. Predicted breeding performance of vacant GULs suitable for raven occupation in intensive study areas: all potential nest-site types

KEY:

- GUL predicted to support small, late clutches
- GUL predicted to support large, late clutches
- GUL predicted to support small, early clutches
- GUL predicted to support large, early clutches

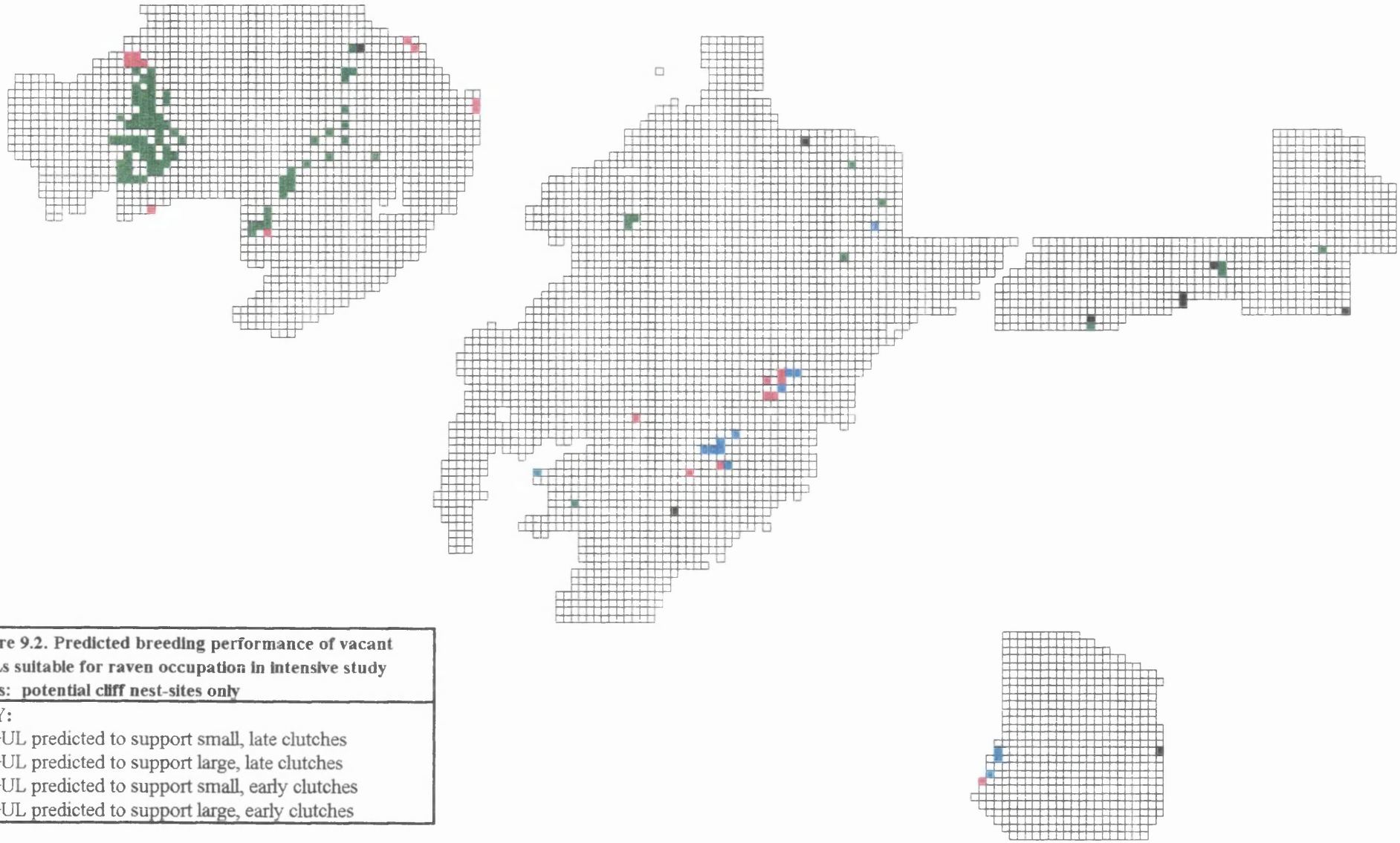

Figure 9.2. Predicted breeding performance of vacant GULs suitable for raven occupation in intensive study areas: potential cliff nest-sites only

KEY:

- GUL predicted to support small, late clutches
- GUL predicted to support large, late clutches
- GUL predicted to support small, early clutches
- GUL predicted to support large, early clutches

intensive study area	estimated number of pairs which could be situated in suitable[1] GULs with predicted early laying of large clutches	estimated number of pairs which could be situated in suitable[1] GULs predicted to be either late laying, small clutches , or both	estimated total number of pairs which could be located in vacant GULs
Lorn	3	8	11
Cowal	1	1	2
Mull	5	8	13
Glens	0	5	5
Total	9	22	31

Table 9.34. Estimated number of pairs unclaimed territories from intensive study areas: potential cliff nest-site only

[1] suitable GULs were those classed as vacant (Chapter 6), containing a potential cliff nest-site (Chapter 7), in habitat suitable for occupancy (Chapter 8), and graded according to suitability for production of large clutches and early laying (this Chapter).

Predicted suitability of deserted territories

In 1990 there were 31 deserted territories (i.e. historically occupied). Of these 21 were in habitat suitable for occupation but 10 were unsuitable, probably due to too much mature conifer plantation in surrounding habitat (see chapter 8). Of the 21 suitable for occupation, many were predicted to be good for breeding: 11 predicted to have large clutches; five early laying; and four both. Only three deserted territories were predicted to be poor for breeding, with late, small clutches. Four of the territories deserted in 1990 were also known to be deserted in 1989, all of these were in habitat suitable for occupation. Two were not vacant because of proximity to nearby ravens. Of the two which remained, one was predicted to be suitable for early laying of large clutches, and the second for late laying of large clutches.

Were apparently suitable gaps in the raven distribution unsuitable for other reasons?

The estimated locations of 'unclaimed territories' may have been unsuitable for reasons other than habitat. Golden eagles are known to displace ravens (Ratcliffe, 1962, Marquiss *et al.*, 1978). In the study area I knew the location of all eagle territories, although I did not know nest locations or occupancy for all of these, as, after consultation with other raptor workers in the area, I avoided them to reduce disturbance. The shortest

distance between occupied golden eagle to occupied raven nests in the study was 0.6km, and the mean distance for 13 nests I did find where nearest occupied raven nest was also known was 2.1km (s.d. = 0.6). Given the confidential nature of eagle nest sites in the study area it was not appropriate to conduct a rigorous exclusion of GULs on the basis of eagle-raven NND similar to that performed between raven sites in Chapter 6. However when considering the best estimates of hypothetical distributions made in Table 9.33, at most only seven locations could be discounted due to proximity to eagles, assuming (generously) that all known eagle territories were occupied in 1990. Considering only those locations estimated to be the most preferred (with potential cliff nest-sites and predicted to lay early, large clutches), only two sites could be excluded due to proximity to eagles.

Potential nest sites predicted in Chapter 7 may have been unsuitable upon closer inspection. This was unlikely to be so for tree nests, considering the small trees used in mid-Argyll and elsewhere. However, large cliffs were apparently preferred and the method used to detect these from Ordinance Survey maps did not distinguish cliff size. Were sites vacant even though located in apparently suitable habitat because of the quality of the potential nest site? This was not the case. Ten of the estimated 31 unclaimed territories with potential cliff sites were predicted to occur in known raven territories deserted in 1990, where old nests had been found. There were no significant differences in cliff nest site measurements between deserted and occupied sites in 1990 (chapter 7). In addition one deserted territory containing a tree site was known in the intensive study areas: this was identified as an unclaimed territory with potential tree nest-site and with habitat suitable for early laying of a large clutch. Cliffs were known from fieldwork (but not measured) in all other locations identified as unclaimed territories and having potential cliff nest-sites, however I find no reason to suspect any of them of being unsuitable sites. For example large clusters of suitable GULs with potential cliff sites were found in Glen More and around Ben Hope on Mull, and in Glen Domhain in Lorn. These areas hold a good selection of tall cliffs.

One unclaimed location could be excluded on grounds of human disturbance as it was on a busy golf course, but no others were near sources of human activity.

After excluding unclaimed territories which could be explained by to proximity to eagles and human disturbance I estimate that the intensive study areas could have held an additional 49 pairs. Using this figure the area held only some 50% of the maximum number of pairs possible. Eight of these locations were predicted to be suitable both for early laying of large clutches and with a potential cliff nest-site. Based on my knowledge of the area I could find no explanation why these sites should be otherwise unsuitable for ravens. It was notable that most unclaimed territories were in inland and not coastal locations. If coastal nesting was preferred to inland, perhaps due to taller nest cliffs or a wider variety of food, then this was perhaps evidence that the most preferred sites were occupied first by new recruits. However, the existence of a large number of vacant locations which were predicted to be suitable for ravens, especially those predicted to be good for breeding, indicated that their numbers in mid-Argyll were not limited by the extent of suitable habitat.

DISCUSSION

Raven breeding performance and habitat

There were many associations between environmental variables from the GIS and breeding performance. Detailed ecological inference based on these differences would be misleading, as many variables were inter-correlated and no account was taken of interactions between variables. Variables were selected for inclusion in predictive multivariate modelling on statistical grounds, or for ease of acquisition, rather than to elucidate ecological relationships. Even had this been the case, interpreting causal relationships by multivariate modelling can be misleading, as discussed in the general introduction to Chapters six to ten. With these caveats in mind, however, it is possible to draw some general conclusions.

In occupied territories, whether or not breeding was attempted was not detectably related to habitat. Timing of breeding was influenced by altitude with early breeding tending to occur at lower elevations and near the coast, presumably due to milder climatic conditions. Timing of laying is governed by stimulation of gonadal development with increasing daylength (Lofts and Murton, 1968), but is also strongly influenced by food

supply through its effect on pre-breeding body condition of the female (Dijkstra *et al.*, 1982; Korpimäki, 1987; Daan *et al.*, 1989). Milder climatic conditions at lower altitudes and towards the coast probably resulted in earlier occurrence of the spring increase in food supplies. Grassland (predominantly sheepwalk) was positively correlated with altitude. This habitat was more useful than summary measures of altitude in predicting laying date, presumably as this provides a biological interpretation of high altitude land rather than one based simply on elevation. Forestry did not detectably influence timing of breeding in mid-Argyll, in contrast to the findings of Marquiss *et al.* (1978). Whilst this difference may be due to only two years data being considered for mid-Argyll, it should be noted that Marquiss *et al.* did not investigate the separate variance explained by amount of forestry surrounding nests once altitude had been accounted for, and in their area forestry planting tended to occur at the highest elevations.

Clutch size appeared to decrease with increasing afforestation around nests in mid-Argyll. However habitat did not appear to influence the number of young fledged. Clutch size in birds is affected by age of the hen, but more strongly by energy reserves and food supply available to her at the time of laying (Dijkstra *et al.*, 1982; Korpimäki, 1987; Daan *et al.*, 1989). Ravens lay very early in the year, and clutch size may be an indication of winter and early spring food conditions. Newton *et al.* (1982) found that annual variations in the mean number of eggs laid per pair were positively correlated with the amount of sheep carrion available in winter/spring. Marquiss *et al.* (1978) found that the percentage frequency of sheep remains in pellets fell with increasing amounts of afforestation. The main detrimental effect of afforestation on ravens may therefore be due to reduced carrion supplies at this critical time of the year.

Breeding attempts tended to fail less near the coast and at lower altitudes perhaps due to milder climatic conditions, or also by benefiting from coastal food supplies. Breeding became less successful with increasing amounts of surrounding land under thicket forestry or *Calluna* bog whilst greater amounts of grassland resulted in improved breeding success. This may be due to greater spring food supplies in grassland compared to *Calluna* or mature forestry. Brood reduction by starvation of the least competitive chicks is the norm in ravens (Davis and Davis, 1986) and is common in birds with asynchronous hatching. However, no relationship

was detected between landcover and fledged brood size. Nevertheless, loss of foraging habitat due to afforestation may have lengthened foraging time, forcing parents to leave the nest unguarded for longer. This may increase the risk of predation, which generally results in complete loss of the nest contents (Davis and Davis, 1986). These suggestions could be investigated by field observations of nest attendance. Though the proportion of many habitats differed between successful and unsuccessful breeding attempts for many radii, these differences were an incomplete explanation of factors responsible for breeding success, as no predictive model could be developed.

Why were ravens absent from apparently suitable locations?

The estimated percentage of unclaimed territories was much greater than could be accounted for by temporary desertion: as reported in Chapter 6, annual occupancy rates averaged over 88% in three long term studies (Ratcliffe, 1962; Dare, 1986; Davis and Davis, 1986). Availability of suitable habitat was not responsible for all of the observed gaps in raven distribution. Over two thirds of territories deserted in 1990 were apparently still suitable for occupancy, and many of these were predicted to have habitat suitable for good breeding. Sites which would be expected to be the most preferred, with good predicted breeding and large, craggy cliffs, away from human disturbance, con-specifics and competitors, remained unoccupied. Some of these had been occupied in the past.

The existence of large amounts of vacant but suitable habitat, and untenanted traditional territories which had suffered relatively little habitat change, suggests that the population is below carrying capacity. What could give rise to failure of ravens to occupy suitable locations? Desertion of traditional territories by ravens and raptors has been frequently linked to declines in food supplies. This may be due to habitat change, or decline in a major prey species for reasons such as depletion by man, or by disease. Lowering of food supplies tends to occur over time however, and generally results in a reduction in breeding performance prior to desertion (Marquiss *et al.*,1978). There was no evidence of poorer breeding in mid-Argyll than elsewhere in Britain (chapter 4). Whilst it is likely that many past traditional territories in mid-Argyll are now vacant because of land-use change, there also appears to have been further losses throughout the area, with no corresponding

decrease in breeding performance. A possible answer may be that there were insufficient recruits to fill vacancies as they arose. The few non-breeders observed in the breeding season (chapter 4) lends support to this. As ravens must be at least three years old to breed (Heinrich, 1990), many of these birds could have been sexually immature, leaving very few potential recruits. This situation could be caused by 1) very rapid turnover of adults occupying territories, outstripping the supply of recruits; 2) high mortality of non-territorial birds resulting in few reaching maturity; or 3) migration of potential recruits away from the area. Evidence to support or dismiss these alternatives is scant. There are large numbers of non-territorial birds in the area in autumn and early winter, for example in 1990, when there were large gatherings of 25-91 ravens reported at several mainland roosts and rubbish tips (Petty, 1991). Non-territorial ravens are not present in these numbers by spring but whether they die or move away is unknown. In an adjacent area of Argyll, large congregations have been reported at sheep and deer carcasses in winter, but no non-territorial birds were observed in this area during the breeding season (Hancox, 1985). These winter flocks may be due to migration from Scandinavia (Bannerman and Lodge, 1953; Coombes, 1948).

Future studies modelling affects of afforestation

Afforestation was clearly detrimental to aspects of raven breeding performance. In Chapter 8 I found 72 locations which were suitable for raven occupancy but which contained only potential nest-sites in mature plantation conifers. In this regard afforestation may have been beneficial to ravens, but interestingly only one of these sites was predicted to be suitable for large clutches. However, the effect of afforestation cannot be studied in isolation from other habitats. As previously discussed, inferential multivariate modelling of habitat suitability requires a mechanistic understanding of the relationship between ravens and their habitat, throughout the year. This would be extremely difficult to obtain. In this regard it may not prove possible to improve upon the correlational approach adopted by Marquiss *et al.* (1978) and Newton *et al.* (1982). Predictive modelling did not require or assume causal relationships and spatial distributions of results with a GIS provided new insights. Breeding success in relation to a more exact measure of habitat fragmentation, especially of forestry blocks, and distribution of these habitats around the nest, would be worthy of investigation.

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CHAPTER 10. CONCLUSIONS

INTRODUCTION

The British uplands are an unique and highly varied landscape dominated by semi-natural or man-made plant communities and which support an avian community with an unusual mixture of species. The semi-natural plant communities are derived mainly from native species but are maintained by traditional land uses, predominantly management for sheep and deer, and raising of game birds. Recent decades have seen major changes in land use over much of these areas, and the loss of natural and semi-natural habitats is giving cause for concern. Changes in habitat due to afforestation with exotic conifers and 'improvement' for agriculture far outweigh all other changes in their impact on the upland bird fauna (Ratcliffe, 1990). Ravens and golden eagles are thought to be particularly vulnerable because they require large foraging areas, food supplies which are maintained by traditional land use, and are unable to hunt in afforested land once the growing trees form a closed canopy.

The two detailed studies which have been made of the impact of afforestation on ravens in Britain produced conflicting results. Marquiss *et al.* (1978) provided convincing evidence that large scale afforestation in the northern Pennines had led to desertion of many traditional territories. This appeared to be due to a reduction in food supply, especially sheep carrion. Newton *et al.* (1982) found no such relationships in central Wales. These contrasting findings emphasise the undoubted complexity of the relationship between ravens, habitat and food supplies. This relationship is very poorly understood as the birds present great difficulties for field observation and experiment. Consequently, a mechanistic understanding of the interaction between habitat, prey and raven population dynamics is unlikely in the foreseeable future. This is a crucial gap in our knowledge as effective conservation measures require predictive models. From this perspective it is important to be able to predict where numbers of ravens will change in relation to land use change; to identify features of land management and habitats that will enhance the survival of the birds and their productivity; and to facilitate better means of monitoring the birds and their habitat. Statistical modelling of observed variation in

bird distribution and breeding performance in relation to observed variation in environment is one method of tackling these issues without the need to understand causality, indeed these techniques are frequently used to help elucidate causal relationships. The issues raised above require not only 'what if?' predictions, but also 'where?'. Geographical Information Systems provided a technique for addressing these spatial problems, and digital terrain modelling and satellite remote sensing the means to provide high resolution information about the environment over the large area required.

RAVEN DISTRIBUTION AND POPULATION DYNAMICS

Reproductive performance was found to be density independent between raven populations in Britain and there was evidence from mid-Argyll and mid-Wales that this relationship holds even at a local level. The evidence indicates that raven breeding distribution in relation to habitats of different quality can best be described by the theoretical *ideal free distribution* of Fretwell and Lucas (1970). They developed two alternative models to explain why individuals settle in less preferred habitat as the population increases. The ideal-free distribution proposes that the suitability of a preferred habitat is negatively related to density, due to increased competition, so that as density increases less suitable habitat become equally attractive. In such a distribution reproductive success will be independent of population density, and as a result, all individuals in the population achieve the same reproductive success, irrespective of their habitat choice . The second model, the *ideal despotic distribution* proposes that some territory holders are able to exclude others from the preferred habitat and force them to settle in less preferred habitat. In an ideal despotic distribution reproductive success will be uniform within habitats, but differ between habitats.

The ideal free distribution should be regarded as a theoretical construct rather than a realistic rule describing habitat selection (Fretwell, 1972, *in* Hobbs and Hanley, 1990). However, as would be predicted from this model, raven populations appear to respond to changed habitat quality by adopting a new distribution of pairs. Given the traditional nature of their territories, preferences for certain nest sites and in some areas inter specific competition for nest-sites with eagles, it is likely that many years will elapse before a new optimal

distribution of pairs can arise. The response time to change is almost certainly slower than the continuing pace of habitat change, and some areas may hold numbers of territories well below the maximum which could be accommodated. Response time will depend upon adult turnover, and the dispersal and recruitment of young birds, parameters which may vary between regions in Britain. Theoretical modelling of the time taken for a new optimum distribution to arise, for different theoretical values of these parameters may be instructive, and have application to other species. Possibilities for measuring adult turnover include: individually marking breeding birds; DNA fingerprinting of chicks (although this may be confounded by extra pair copulations and egg dumping); for the hen, analysis of egg markings (*sensu* Thomas and Thompson, 1987); or identification of individuals by sonographic analysis of vocalisations. Studies of dispersion and recruitment will have to rely upon recoveries of marked birds. The possibility of some areas acting as a source of recruits and others as sinks warrants further investigation. Ringing of nestlings and non-territorial birds in winter flocks (for example cannon-netting over carcasses) should be encouraged. The number of recoveries of British ringed ravens is now approaching 500 birds: a new analysis of these data, especially if combined with ringing effort and population density, would be timely.

Variation in habitat quality is manifest in different raven densities between areas. Detrimental changes in land use may influence breeding performance prior to abandonment of the territory. Presumably the cost to fitness this incurs is less than that resulting from relocating, until a threshold is reached. However, in short-term studies or infrequent monitoring, reduced breeding performance due to land use change is likely to be obscured by natural variation in breeding performance in any year. Monitoring of populations should therefore aim to record occupancy for complete distributions in larger areas, rather than recording details of breeding performance for a smaller number of pairs. Long-term monitoring of (large) sample plots in different populations should be established. In several areas ravens are already monitored, but procedures should be standardised.

MODELLING HABITAT SUITABILITY FOR OCCUPANCY AND BREEDING PERFORMANCE

The principal aim of this thesis was to find ways of predicting the occurrence and breeding performance of ravens in relation to habitat features in mid-Argyll, both quantitatively and spatially. This required the definition of a 'location' and measurement of habitat surrounding it. Defining 'location' means adopting a minimum unit of area in which observations can be placed, for example presence or absence of raven nests. Locations are most conveniently represented as a grid. Many previous studies used the unit of location as the unit in which to sample habitat. Such an approach is unlikely to uncover anything other than general habitat associations where the sampling /location unit is much larger than the species' home range. Alternatively, where these units are much smaller than home range, habitat associations are more likely to be concerned with nest site selection, with little regard for the suitability of surrounding areas to maintain the birds. Ideally, the sampling unit should therefore approximate to the home range size of the bird. However, if the scale at which habitat fragmentation is important to the birds is below the scale of the sampling unit, then this same unit cannot be used as the unit of location. This was the case for ravens in mid-Argyll, where home range size was likely to be over 6km in diameter. In this thesis I solved this problem by choosing a small unit of location of 500m x 500m (grid unit of location = GUL), and measured habitats in much larger areas around these. The low density of ravens in mid-Argyll required a very large study area to include a sufficient number of raven territories for analysis. The large number of GULs within this area (9677), and the size of the area in which habitat needed to be measured around these (up to 100km^2), meant that this was possible only by using computerised techniques. The power of the GIS procedures developed in this thesis also allowed measurement of habitat in incrementally larger regions around locations. This helped significantly with modelling since variance in the distribution of habitat types could be incorporated in to the models.

Most studies which seek to determine habitat suitability or selection for birds, compare habitat in regions around a sample of nests with that where birds are absent. This makes the assumption that unoccupied locations are unsuitable. In many cases this may be justified, for instance where sexually mature pairs are

observed to be excluded from breeding. However, in other cases there are good reasons to suspect that habitat may not be the main limiting factor governing numbers and distributions, e.g. where human persecution controls population size. In addition, for territorial birds such as ravens, if units of location are necessarily smaller than home range, then many will be unoccupied solely because of the influence of neighbouring pairs rather than due to habitat. Gaps in a species distribution frequently occur, both at local and regional scales. Formal identification of gaps, and trying to determine why they occur where they do, has been surprisingly neglected (Lawton and Woodroffe, 1991). To my knowledge this study is the first to address these issues directly in predictive spatial modelling of habitat suitability .

IDENTIFICATION OF GAPS IN THE DISTRIBUTION OF RAVENS

Gaps were defined quite simply by drawing circular exclusion zones around each occupied site using a radius equal to regional mean nearest neighbour distance. This showed that there were many locations where a new territories could have been fitted between existing pairs. Ideally one would use home range boundaries but 1) these are unlikely ever to be available for ravens over a wide area and 2) the nature of spacing behaviour in ravens, being apparently by mutual avoidance rather than defended boundaries, make this a valid proxy measure. This approach could be extended by modelling nearest neighbour distance to habitat but 1) there was little variation in inter-nest distance across the study area, and 2) individual inter-nest distances may have been strongly affected by the distribution of gaps in raven distribution. A more useful approach may be to consider distances to and between all surrounding pairs (Theissien neighbours) in relation to the distribution of habitats, but this was beyond the scope of the present study.

PREDICTING THE OCCURRENCE OF POTENTIAL NEST SITES

Occupancy, breeding attempt, and breeding performance were not affected by differences in nest-site features in mid-Argyll. This may have been partly due to the wide availability of high quality sites and partly to the very low levels of human disturbance. Thus prediction of nest-site availability did not need to consider the quality of the site, merely presence or absence. This was reliably ascertained from published maps, and was

easily calculated for all GULs using the GIS. There were, however, indications from field observations and published accounts from elsewhere that ravens exhibit strong preferences for certain types of nest-sites and that sites could possibly be ranked in order of preference. This information was required to be able to predict which of several alternatives ravens would be predicted to occupy. Unfortunately it was not possible to predict cliff height with sufficient precision from the digital terrain model at the resolution used and the effort required to provide a model of higher resolution, or field measurement of a sufficient number of sites over a wide enough area was prohibitive. Though most areas contained potential nest-sites, 45% of GULs could be excluded as potential locations for raven occupancy, solely on the basis of probable suitability for nesting. Potential nest-site availability did not account for the gaps in raven distribution within intensive study areas. This was not unexpected given the rugged terrain, and the widely reported willingness of ravens to accept apparently poor sites if apparently preferred sites are unavailable. Most gaps contained some GULs with cliffs, many of which were known from field work and I would subjectively rank many of these as being the most preferred type of site. Clearly, nest-site availability did not influence numbers and breeding success for ravens in mid-Argyll, and is unlikely to do so in most areas of great Britain, except where mediated by human persecution.

PREDICTING LOCATION SUITABILITY FOR BREEDING RAVENS

It was known from previous long-term studies that the distribution of breeding ravens remains remarkably stable in the absence of habitat change, and that afforestation often rendered previously occupied locations unsuitable. However, previous studies have not been able to quantify the amount of ground lost to ravens due to these activities. This was possible in the present study by using multivariate predictive modelling of suitability in combination with a GIS to map suitability on a GUL basis. In mid-Argyll 43% of locations which also contained a potential nest-site were found to be unsuitable for occupation by ravens due solely to afforestation, using principal components analysis. This was a much larger figure than the percentage of land under conifers and demonstrated that the wildlife value of an area can be more severely affected than summary figures of the amount of ground lost may indicate. Locations in large forest blocks were unsuitable, but along

forestry edges or where forest was fragmented, these often remained within the tolerance limits observed in the intensive study areas. However, the principal components analysis took no account of variations in the quality of the remaining habitat, which may also influence suitability.

As habitats which were important to the birds were not known, evaluation of the quality of the habitat to ravens was assessed by predicting parameters of breeding performance using these variables. It was possible to predictively model only clutch size and laying date from a very large range of habitat variables. Both of these parameters are determined by food supplies available to the female before laying. In the case of ravens which nest at the end of winter, they may be regarded as indices of winter food supply. Although models were not constructed to be inferential, it was apparent that laying date was most strongly influenced by altitude and distance the coast, which implies a climatic effect, whereas clutch size was reduced if surrounding land was afforested, which suggests reduced winter food availability. Many locations were classed as suitable which contained only potential nest-sites provided by the forestry, and in this way fragmented forestry may actually benefit ravens. However nearly all of these were predicted to be unsuitable for the production of large clutches. The variables considered could not be used to construct a robust predictive model of breeding success, even though there were many univariate differences between successful and failed pairs. It is likely that perturbations in breeding success due to chance events obscured real differences due to habitat and that data from a long term study would have enabled predictive models to be made.

A prediction of an ideal free distribution is that all individuals in the population achieve the same reproductive success, irrespective of their habitat choice. However, as raven sites are very traditional, habitat choice may often have been made before detrimental land-use changes occurred. Where this has occurred after an ideal free distribution based on previous habitat had become established we might predict that reproductive success will vary, dependent upon the amount of detrimental land-use change, and the habitats it replaced. Thus the hypothesis cannot be tested directly in a short term study as it requires long term data from years before to many years after land use has changed.

WHY WERE THERE GAPS IN THE RAVEN DISTRIBUTION?

There were many locations in intensive study areas which could not be statistically distinguished from occupied raven sites on the basis of nest-site availability or habitat suitable for breeding performance, and many were also predicted to have the best breeding performance. Very few of these could be eliminated because of proximity to human disturbance or competition from eagles. There were no obvious reasons for the absence of ravens from these areas, and other species such as hooded crows and buzzards were abundant and thriving, indicating that factors difficult to detect, such as poisoning or predation, were not to blame. There was thus the clear suggestion that many locations were vacant simply because there were not ravens to fill them. This conclusion is supported by the very low numbers of non-territorial birds present during the breeding season. Field studies of recruitment would be extremely difficult and would require a long term study. However, the conclusion reached in this study could be tested by a removal experiment, in which occupied territories are made vacant by capture (and release elsewhere) of occupants. This should be done in mid-Wales and mid-Argyll. Sites in mid-Wales would be predicted to be reoccupied by new birds relatively quickly, but most sites in mid-Argyll would remain vacant. In the meantime, I conclude that in mid-Argyll, because the raven population is well below the maximum numbers expected, the availability of suitable habitat, and particularly the present degree of afforestation, is not limiting this population, but could set an upper limit to any increase in numbers.

STATISTICAL AND SPATIAL MODELLING PROCEDURES

The initial assumption that ravens were not at carrying capacity in the study area was proved correct, and the models derived by usual procedures to infer and predict habitat suitability based upon statistical comparison between occupied and unoccupied locations would have been severely weakened. Studies which wish to use these techniques, which are, after all, considerably simpler to design and conduct, should therefore provide justification for the assumption that all suitable habitat is occupied. In addition, it is clear from the statistical literature that inference of causal relationships from multivariate analysis is very liable to misinterpretation unless conducted with great rigour. Where statistical assumptions are believed violated (and this should be

assumed unless proved otherwise with most field data) validation techniques must be employed. In this study I used methods which were testable either by split sample validation, or by checking predictions on data from test areas. Ecological inference was limited by the design of statistical procedures, but by overlaying results in a GIS and viewing them in their spatial context valuable insights were made. In addition the modelling revealed many potential new avenues to explore, often using the same base data from the GIS. For example forest fragmentation would be worthy of a more detailed investigation than undertaken here. Macros could be written to take complex measurements from the classified Landsat image (to enable, for example, calculation of fractal dimension) which would be very difficult by any other technique. In addition many of the models developed here would have been improved by using a longer run of raven data.

Predictive models are likely to be more useful to conservation managers, and possibly instructive to ecologists, than inferential modelling. This is because they can establish mathematical relationships between a species and its environment even when underlying relationships are unknown. Whilst ecological relationships are of undoubted interest they are inevitably highly complex, and likely to vary considerably over a species range. They therefore require many years to establish, and are extremely difficult to apply in a predictive manner. In addition the data they require is likely to be difficult and expensive to collect, as most relationships will inevitably involve prey abundance and availability. Prey abundance/availability is ill suited as a variable for predictive modelling as: 1) it cannot be measured after a change in habitat until that change has occurred; and 2) the alternative method of predicting prey abundance based on habitat makes it redundant. I have demonstrated that predictive models for distribution and breeding performance can be derived for a species with an undoubtedly complex ecology. In addition, these models used widely available, or relatively easily obtained, spatial data. The increasing availability of digital information can only improve this situation. These predictive models were also given power by use of a GIS enabling results to be viewed in their spatial context. By answering the 'where' question we may shed hitherto unregarded light on the 'why'.

PREDICTING THE EFFECT OF FUTURE LAND USE CHANGES ON RAVENS IN MID-ARGYLL

The models derived in this study could serve as a basis to predict the effect on ravens which may occur due to changing land use. This would be done by simulating the change in the GIS. For example, if the boundaries of a proposed new forestry block were available these would be digitised and land use maps modified. The new land covers around ravens in the area would then be measured and occupancy and breeding performance calculated. In this way more specific estimates of the effect of the proposed change could be made than hitherto possible. This method obviously requires that the new land use, and the habitats it replaces, are used as variables in predictive models, and a suite of models which use different variables from those used here, may be required. The base data in the GIS can be used in many ways, and different data sets for modelling could be derived for a range of species, either independently or in a community approach. Indeed the GIS used here was also used for a similar study of buzzards (Austin *et al.*, in prep.), which again, although presenting different problems for study design and analysis, resulted in good predictive models. A suite of models for a whole range of animals could thus be applied in simulations of land use change. This approach clearly has broad potential for conservation managers and countryside planners.

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TABLE OF TABLES

APPENDIX. CORRELATION MATRICES FOR CHAPTER 9.

APPENDIX. CORRELATION MATRICES FOR CHAPTER 9

Variables which differed between groups of territories with different breeding performance were given in Tables 9.4 to 9.7. Subsets of these variables were chosen for inclusion based on the significance of the difference and by visual reference to correlation matrices. These are presented in this appendix. Codes are used in matrices column and row headings, these are derived from a base code (see overleaf) with a code for radius appended. Codes for radii were:

_0 = 0.5km

_1 = 1km

_2 = 2km

_3 = 3km

_4 = 4km

_5 = 5km

variable type	base code used in correlation matrices	Description of variable
HUMAN	ROADS_	length of metalled roads
BOUNDARY LENGTHS	COA_	length of coastline (m)
	LMAT_	length of thicket stage conifer plantation boundary (m)
	LPRE_	length of pre-thicket stage conifer plantation boundary, excluding that abutting thicket stage conifer plantation (m)
	LFOR_	length of conifer plantation boundary (m)
	LWOO_	length of all woodland and conifer plantation boundary abutting open-land landcover classes (m)
	LLAN_	length of all boundaries between classes excluding those abutting fresh and salt water (m)
	LTOT_	length of all boundaries between all classes (m)
PROPORTION OF TOTAL AREA	GD_3_	thicket conifer plantation
	GD_4_	pre-thicket stage conifer plantation/scrub
	GD_5_	*Calluna* bog
	GD_6_	mixed bog
	GD_9_	perennial grassland
	GD_12_	fresh water
	GD_13_	salt water
PROPORTION OF TOTAL AREA (COMBINED CATEGORIES)	GAFF_	total forestry: thicket + pre-thicket conifer plantation
	GWET_	total bog and wet heath: *Calluna* + mixed heath + wet heath
	GBOG_	total bog : *Calluna* + mixed heath
	GGRA_	total grassland: wet heath + perennial grassland + agricultural
	GWGRA_	total semi-natural grassland: wet heath + perennial grasslands
PROPORTION OF LAND	LN_3_	thicket conifer plantation
	LN_4_	*Calluna* bog
	LN_5_	mixed bog
	LN_10_	deciduous woodland
PROPORTION OF LAND (COMBINED CATEGORIES)	AFF_	total forestry: thicket + pre-thicket conifer plantation
	GRA_	total grassland: wet heath + perennial grassland + agricultural
	WGRA_	total semi-natural grassland: wet heath + perennial grasslands
TERRAIN	MAXAL_	maximum altitude within radius
	RANAL_	altitude range within radius
	MODAL_	modal altitude within radius
	MEDAL_	median altitude within radius
	MINSL_	minimum slope within radius
	MAXSL_	maximum slope within radius
	RANSL_	slope range within radius
	MEDSL_	median slope within radius
	MINRUG_	minimum ruggedness index within radius
	NOASP_	proportion of land with no aspect
	EAST_	proportion of land in radius facing east
	RIV_	length of river (>8m wide) within radius

Appendix key: Base codes for environmental variables used in correlation matrices for Chapter 9
Variables are grouped by type, alternate shading separates types for clarity

	COA_5	GD13_5	GD12_1	GD12_2	GD12_3	GD12_4	GD12_5	AFF_4	AFF_5	GAFF_4	GAFF_5	GD3_3	GD3_4	GD3_5	LN3_3	LN3_4	LN3_5	GD5_1	GD5_2	GD5_3	GD5_4	GD5_5	LN5_2	LN5_3	LN5_4	LN5_5	GRA_5	WGR_4	WGR_5	GD9_1	LTOT_1	LTOT_2	LTOT_3	LTOT_4	LLAN_1	LLAN_2	LLAN_3	LLAN_5	LWOO_4	LPRE_4	MODAL_0	MODAL_1
COA_5	1.00																																								
GD13_5	0.82	1.00																																							
GD12_1	-0.32	-0.33	1.00																																						
GD12_2	-0.40	-0.40	0.60	1.00																																					
GD12_3	-0.44	-0.46	0.48	0.88	1.00																																				
GD12_4	-0.56	-0.58	0.52	0.77	0.94	1.00																																			
GD12_5	-0.69	-0.67	0.49	0.64	0.81	0.92	1.00																																		
AFF_4	-0.29	-0.46	0.45	0.38	0.46	0.52	0.50	1.00																																	
AFF_5	-0.28	-0.45	0.49	0.34	0.42	0.50	0.48	0.97	1.00																																
GAFF_4	-0.49	-0.63	0.50	0.44	0.53	0.62	0.64	0.95	0.93	1.00																															
GAFF_5	-0.50	-0.65	0.57	0.43	0.50	0.60	0.62	0.94	0.95	0.98	1.00																														
GD3_3	-0.48	-0.50	0.46	0.52	0.59	0.67	0.59	0.79	0.72	0.86	0.78	1.00																													
GD3_4	-0.52	-0.56	0.51	0.50	0.59	0.64	0.66	0.83	0.79	0.90	0.86	0.97	1.00																												
GD3_5	-0.56	-0.60	0.61	0.50	0.59	0.67	0.68	0.84	0.83	0.92	0.92	0.90	0.97	1.00																											
LN3_3	-0.41	-0.44	0.43	0.51	0.57	0.54	0.53	0.82	0.75	0.84	0.77	0.98	0.94	0.87	1.00																										
LN3_4	-0.46	-0.50	0.51	0.50	0.58	0.61	0.60	0.86	0.82	0.90	0.86	0.96	0.99	0.95	0.96	1.00																									
LN3_5	-0.50	-0.57	0.59	0.47	0.55	0.63	0.63	0.87	0.86	0.92	0.92	0.88	0.96	0.99	0.87	0.96	1.00																								
GD5_1	-0.46	-0.33	0.10	0.06	0.26	0.37	0.40	0.33	0.36	0.41	0.43	0.37	0.40	0.43	0.32	0.36	0.40	1.00																							
GD5_2	-0.57	-0.51	0.14	0.08	0.26	0.39	0.43	0.41	0.44	0.52	0.54	0.38	0.42	0.47	0.32	0.37	0.44	0.88	1.00																						
GD5_3	-0.63	-0.58	0.21	0.16	0.28	0.39	0.47	0.46	0.47	0.59	0.59	0.44	0.48	0.52	0.38	0.43	0.48	0.70	0.94	1.00																					
GD5_4	-0.67	-0.62	0.20	0.16	0.27	0.37	0.52	0.48	0.49	0.61	0.61	0.44	0.48	0.51	0.38	0.44	0.47	0.61	0.86	0.97	1.00																				
GD5_5	-0.67	-0.63	0.21	0.20	0.28	0.37	0.52	0.53	0.52	0.64	0.64	0.47	0.50	0.53	0.43	0.47	0.50	0.56	0.81	0.94	0.98	1.00																			
LN5_2	-0.41	-0.28	0.11	0.05	0.22	0.33	0.32	0.36	0.37	0.43	0.43	0.30	0.34	0.35	0.25	0.30	0.32	0.87	0.94	0.88	0.79	0.71	1.00																		
LN5_3	-0.49	-0.35	0.18	0.09	0.21	0.31	0.37	0.40	0.41	0.49	0.49	0.36	0.39	0.43	0.30	0.36	0.39	0.68	0.89	0.95	0.90	0.87	0.91	1.00																	
LN5_4	-0.51	-0.31	0.15	0.10	0.20	0.27	0.38	0.39	0.38	0.48	0.47	0.37	0.38	0.39	0.33	0.34	0.36	0.60	0.83	0.92	0.91	0.89	0.83	0.96	1.00																
LN5_5	-0.49	-0.33	0.15	0.10	0.18	0.25	0.37	0.49	0.46	0.56	0.51	0.40	0.41	0.40	0.37	0.40	0.38	0.53	0.76	0.88	0.93	0.92	0.74	0.91	0.96	1.00															
GRA_5	0.47	0.36	-0.30	-0.24	-0.32	-0.39	-0.43	-0.53	-0.52	-0.61	-0.63	-0.54	-0.57	-0.61	-0.53	-0.58	-0.61	-0.50	-0.64	-0.72	-0.70	-0.72	-0.56	-0.74	-0.74	-0.67	1.00													
WGR_4	0.12	0.00	-0.19	-0.16	-0.24	-0.28	-0.28	-0.60	-0.56	-0.56	-0.54	-0.45	-0.47	-0.45	-0.47	-0.50	-0.47	-0.44	-0.55	-0.59	-0.67	-0.59	-0.59	-0.70	-0.71	-0.71	0.82	1.00												
WGR_5	0.13	0.09	-0.24	-0.12	-0.18	-0.24	-0.25	-0.68	-0.68	-0.64	-0.62	-0.44	-0.49	-0.49	-0.46	-0.52	-0.51	-0.43	-0.56	-0.64	-0.65	-0.66	-0.59	-0.72	-0.73	-0.76	0.77	0.95	1.00											
GD9_1	-0.18	-0.38	0.24	0.19	0.20	0.25	0.35	0.64	0.70	0.63	0.67	0.38	0.48	0.52	0.39	0.48	0.54	-0.06	0.09	0.18	0.29	0.34	0.04	0.13	0.22	0.32	-0.17	-0.23	-0.37	1.00										
LTOT_1	-0.47	-0.63	0.21	0.26	0.45	0.53	0.60	0.43	0.47	0.49	0.53	0.31	0.37	0.44	0.31	0.37	0.43	0.58	0.66	0.59	0.61	0.60	0.60	0.54	0.50	0.50	-0.45	-0.42	-0.46	0.34	1.00									
LTOT_2	-0.66	-0.77	0.20	0.23	0.42	0.55	0.70	0.51	0.53	0.62	0.65	0.40	0.47	0.54	0.37	0.44	0.52	0.52	0.71	0.73	0.76	0.77	0.57	0.61	0.56	0.59	-0.52	-0.37	-0.44	0.47	0.89	1.00								
LTOT_3	-0.68	-0.84	0.33	0.31	0.44	0.58	0.73	0.60	0.62	0.73	0.76	0.48	0.56	0.63	0.43	0.52	0.61	0.53	0.73	0.78	0.81	0.81	0.57	0.63	0.57	0.60	-0.54	-0.38	-0.47	0.51	0.78	0.96	1.00							
LTOT_4	-0.67	-0.87	0.35	0.33	0.42	0.56	0.70	0.63	0.64	0.76	0.78	0.50	0.58	0.65	0.45	0.54	0.63	0.60	0.71	0.79	0.83	0.83	0.54	0.63	0.60	0.61	-0.56	-0.40	-0.49	0.52	0.73	0.90	0.98	1.00						
LLAN_1	-0.53	-0.59	0.15	0.24	0.44	0.53	0.61	0.41	0.45	0.48	0.53	0.32	0.38	0.44	0.31	0.37	0.43	0.59	0.68	0.62	0.63	0.63	0.59	0.54	0.49	0.50	-0.45	-0.37	-0.42	0.34	0.99	0.92	0.81	0.75	1.00					
LLAN_2	-0.66	-0.77	0.20	0.23	0.42	0.55	0.70	0.51	0.53	0.63	0.66	0.40	0.48	0.54	0.37	0.45	0.53	0.54	0.73	0.74	0.77	0.77	0.58	0.62	0.57	0.59	-0.53	-0.38	-0.45	0.45	0.89	1.00	0.95	0.90	0.92	1.00				
LLAN_3	-0.72	-0.87	0.31	0.30	0.42	0.57	0.72	0.57	0.59	0.71	0.74	0.48	0.56	0.63	0.42	0.51	0.61	0.54	0.74	0.79	0.82	0.82	0.57	0.63	0.58	0.61	-0.54	-0.34	-0.44	0.48	0.77	0.95	1.00	0.98	0.81	0.95	1.00			
LLAN_5	-0.70	-0.89	0.35	0.35	0.40	0.52	0.66	0.63	0.64	0.77	0.79	0.54	0.60	0.66	0.49	0.56	0.64	0.47	0.68	0.77	0.83	0.83	0.50	0.61	0.59	0.61	-0.56	-0.38	-0.47	0.50	0.69	0.87	0.95	0.99	0.71	0.87	0.95	1.00		
LWOO_4	-0.36	-0.62	0.36	0.31	0.36	0.46	0.54	0.84	0.84	0.86	0.87	0.53	0.60	0.66	0.53	0.61	0.67	0.30	0.50	0.60	0.66	0.74	0.42	0.53	0.53	0.64	-0.54	-0.56	-0.68	0.72	0.68	0.71	0.80	0.84	0.67	0.71	0.77	0.83	1.00	
LPRE_4	-0.38	-0.41	0.26	0.47	0.68	0.65	0.54	0.69	0.63	0.74	0.67	0.81	0.79	0.76	0.79	0.78	0.75	0.53	0.52	0.49	0.41	0.43	0.44	0.43	0.36	0.34	-0.52	-0.43	-0.40	0.16	0.39	0.40	0.44	0.45	0.40	0.42	0.44	0.45	0.47	1.00
MODAL_0	-0.57	-0.62	0.18	0.06	0.02	0.09	0.23	0.29	0.38	0.41	0.51	0.46	0.47	0.57	0.40	0.42	0.53	0.37	0.46	0.50	0.50	0.62	0.32	0.37	0.33	0.34	-0.40	-0.10	-0.20	0.08	0.18	0.36	0.50	0.53	0.26	0.38	0.53	0.57	0.24	0.32
MODAL_1	-0.51	-0.40	0.16	0.42	0.35	0.26	0.36	0.31	0.30	0.44	0.43	0.66	0.57	0.55	0.61	0.53	0.49	0.28	0.34	0.45	0.48	0.51	0.27	0.37	0.41	0.41	-0.52	-0.29	-0.30	0.10	0.15	0.26	0.33	0.36	0.19	0.27	0.35	0.42	0.16	0.48
ROADS_0	0.30	0.10	-0.15	-0.23	-0.29	-0.30	-0.18	-0.22	-0.25	-0.21	-0.22	-0.24	-0.25	-0.25	-0.25	-0.25	-0.24	-0.23	-0.20	-0.18	-0.15	-0.12	-0.25	-0.23	-0.23	-0.20	0.20	0.22	0.22	-0.19	-0.12	-0.14	-0.12	-0.08	-0.15	-0.14	-0.14	-0.07	-0.06	-0.19

	MODAL_1	ROADS_0
	1.00	
	0.63	1.00

Appendix 1.1. Correlation matrix of habitat variables with significantly different medians between territories where breeding attempts were successful or failed (see Table 9.4)

	AFF_1	GAFF_1	GD3_1	LN3_1	GD4_4	GD4_5	LN4_5	LFOR_1	LFOR_4	LMAT_4
AFF_1	1.00									
GAFF_1	0.98	1.00								
GD3_1	0.60	0.69	1.00							
LN3_1	0.67	0.75	1.00	1.00						
GD4_4	0.76	0.83	0.75	0.77	1.00					
GD4_5	0.64	0.69	0.64	0.65	0.97	1.00				
LN4_5	0.67	0.73	0.63	0.65	0.97	0.97	1.00			
LFOR_1	0.87	0.92	0.58	0.62	0.86	0.75	0.81	1.00		
LFOR_4	0.54	0.64	0.59	0.59	0.89	0.89	0.94	0.80	1.00	
LMAT_4	0.61	0.70	0.61	0.61	0.96	0.97	0.98	0.82	0.96	1.00
NOASP_1	-0.23	-0.23	-0.43	-0.44	-0.31	-0.32	-0.29	-0.18	-0.27	-0.27

Appendix 1.2. Correlation matrix of habitat variables with significantly different medians between territories with small or large clutch size (see Table 9.5)

	MIN_SLO_0	MIN_RUG_0	EAST_0
MIN_SLO_0	1		
MIN_RUG_0	0.53	1.00	
EAST_0	0.43	0.41	1.00

Appendix 1.3. Correlation matrix of habitat variables with significantly different medians between territories with small or large fledged brood size (see Table 9.6)

	GD13_1	GD13_2	GD13_3	GD13_4	GD13_5	COA_1	COA_2	COA_3	COA_4	COA_5	GBOG_3	GBOG_4	GBOG_5	GWET_3	GWET_4	GD5_2	GD5_3	GD5_4	GD6_4	GGRA_2	GGRA_3	GGRA_4	GGRA_5	GWGR_2	GWGR_3	GWGR_4	GWGR_5	LN10_2	LN10_3	LN10_4	LTOT_3	MAXAL_0	MAXAL_1	MAXAL_2	MEDAL_0	MEDAL_1	MEDAL_2	MODAL_0	MODAL_2	MEDSL_2	MODSL_1	MODSL_2	RANSL_2
GD13_1	1.00																																										
GD13_2	0.98	1.00																																									
GD13_3	0.93	0.98	1.00																																								
GD13_4	0.91	0.96	0.99	1.00																																							
GD13_5	0.89	0.95	0.98	0.99	1.00																																					
COA_1	0.93	0.91	0.86	0.83	0.80	1.00																																				
COA_2	0.85	0.85	0.84	0.76	0.72	0.93	1.00																																			
COA_3	0.85	0.87	0.87	0.79	0.74	0.88	0.97	1.00																																		
COA_4	0.80	0.85	0.85	0.81	0.79	0.81	0.90	0.95	1.00																																	
COA_5	0.78	0.82	0.82	0.79	0.78	0.77	0.87	0.93	0.99	1.00																																
GBOG_3	-0.64	-0.70	-0.67	-0.64	-0.62	-0.77	-0.83	-0.84	-0.84	-0.83	1.00																															
GBOG_4	-0.61	-0.70	-0.69	-0.68	-0.68	-0.74	-0.80	-0.83	-0.85	-0.85	0.96	1.00																														
GBOG_5	-0.67	-0.76	-0.74	-0.73	-0.79	-0.74	-0.79	-0.82	-0.86	-0.85	0.88	0.96	1.00																													
GWET_3	-0.43	-0.48	-0.46	-0.41	-0.35	-0.56	-0.61	-0.61	-0.51	-0.48	0.66	0.65	0.57	1.00																												
GWET_4	-0.44	-0.49	-0.47	-0.43	-0.38	-0.56	-0.59	-0.60	-0.52	-0.49	0.65	0.66	0.60	0.99	1.00																											
GD5_2	-0.48	-0.52	-0.56	-0.57	-0.50	-0.47	-0.49	-0.52	-0.53	-0.53	0.50	0.54	0.49	-0.08	-0.10	1.00																										
GD5_3	-0.48	-0.53	-0.57	-0.57	-0.56	-0.47	-0.50	-0.54	-0.58	-0.58	0.50	0.55	0.59	-0.12	-0.13	0.95	1.00																									
GD5_4	-0.49	-0.54	-0.59	-0.60	-0.59	-0.47	-0.50	-0.55	-0.62	-0.62	0.51	0.60	0.62	-0.10	-0.09	0.88	0.97	1.00																								
GD6_4	-0.48	-0.55	-0.52	-0.50	-0.47	-0.65	-0.71	-0.71	-0.70	-0.68	0.87	0.88	0.80	0.87	0.88	0.14	0.10	0.15	1.00																							
GGRA_2	-0.58	-0.60	-0.61	-0.58	-0.55	-0.53	-0.50	-0.49	-0.39	-0.36	0.27	0.30	0.35	0.62	0.60	-0.04	-0.02	0.06	0.35	1.00																						
GGRA_3	-0.55	-0.60	-0.66	-0.65	-0.61	-0.44	-0.43	-0.45	-0.39	-0.37	0.24	0.31	0.33	0.62	0.63	-0.01	-0.03	0.03	0.37	0.91	1.00																					
GGRA_4	-0.57	-0.63	-0.66	-0.70	-0.69	-0.48	-0.39	-0.42	-0.39	-0.36	0.24	0.32	0.36	0.60	0.62	-0.03	-0.07	0.02	0.39	0.82	0.97	1.00																				
GGRA_5	-0.61	-0.66	-0.66	-0.70	-0.75	-0.52	-0.43	-0.45	-0.46	-0.45	0.27	0.33	0.49	0.60	0.64	-0.06	-0.10	-0.03	0.44	0.74	0.91	0.98	1.00																			
GWGR_2	-0.59	-0.63	-0.63	-0.60	-0.57	-0.59	-0.60	-0.59	-0.50	-0.46	0.41	0.44	0.48	0.75	0.71	-0.01	0.02	0.09	0.51	0.97	0.88	0.78	0.72	1.00																		
GWGR_3	-0.60	-0.65	-0.68	-0.66	-0.62	-0.58	-0.58	-0.58	-0.51	-0.48	0.44	0.48	0.49	0.80	0.79	0.00	-0.01	0.05	0.58	0.92	0.96	0.91	0.87	0.94	1.00																	
GWGR_4	-0.62	-0.68	-0.70	-0.71	-0.69	-0.60	-0.55	-0.56	-0.51	-0.48	0.43	0.48	0.51	0.79	0.80	-0.03	-0.06	0.01	0.60	0.84	0.94	0.96	0.95	0.86	0.97	1.00																
GWGR_5	-0.62	-0.68	-0.66	-0.67	-0.73	-0.59	-0.53	-0.54	-0.54	-0.52	0.42	0.46	0.59	0.78	0.81	-0.08	-0.12	-0.06	0.63	0.74	0.88	0.93	0.97	0.76	0.91	0.98	1.00															
LN10_2	0.27	0.31	0.37	0.38	0.35	0.33	0.47	0.49	0.50	0.51	-0.41	-0.46	-0.46	-0.32	-0.30	-0.28	-0.31	-0.35	-0.37	-0.30	-0.31	-0.25	-0.22	-0.35	-0.36	-0.30	-0.25	1.00														
LN10_3	0.31	0.38	0.42	0.44	0.46	0.36	0.47	0.50	0.54	0.55	-0.47	-0.55	-0.60	-0.39	-0.39	-0.30	-0.33	-0.38	-0.45	-0.34	-0.37	-0.31	-0.31	-0.42	-0.43	-0.38	-0.35	0.95	1.00												
LN10_4	0.43	0.50	0.55	0.48	0.49	0.43	0.54	0.58	0.60	0.62	-0.52	-0.56	-0.61	-0.43	-0.42	-0.37	-0.38	-0.41	-0.47	-0.39	-0.43	-0.32	-0.33	-0.47	-0.51	-0.41	-0.40	0.88	0.95	1.00											
LTOT_3	-0.74	-0.77	-0.78	-0.82	-0.83	-0.68	-0.57	-0.60	-0.65	-0.65	0.52	0.56	0.63	-0.08	-0.03	0.79	0.83	0.82	0.20	0.18	0.16	0.28	0.35	0.17	0.14	0.23	0.26	-0.21	-0.27	-0.30	1.00										
MAXAL_0	-0.68	-0.72	-0.72	-0.68	-0.72	-0.71	-0.73	-0.72	-0.70	-0.69	0.59	0.70	0.68	0.52	0.53	0.44	0.42	0.44	0.61	0.46	0.48	0.41	0.45	0.56	0.57	0.51	0.53	-0.42	-0.48	-0.54	0.50	1.00									
MAXAL_1	-0.63	-0.70	-0.69	-0.69	-0.73	-0.67	-0.68	-0.68	-0.67	-0.67	0.61	0.73	0.71	0.61	0.62	0.37	0.34	0.36	0.69	0.48	0.52	0.47	0.50	0.58	0.62	0.58	0.60	-0.38	-0.46	-0.53	0.41	0.97	1.00								
MAXAL_2	-0.59	-0.67	-0.67	-0.65	-0.65	-0.68	-0.71	-0.71	-0.67	-0.66	0.70	0.79	0.78	0.73	0.74	0.36	0.31	0.31	0.80	0.46	0.51	0.46	0.46	0.58	0.65	0.62	0.61	-0.46	-0.56	-0.64	0.31	0.89	0.94	1.00							
MEDAL_0	-0.69	-0.72	-0.72	-0.69	-0.70	-0.72	-0.72	-0.72	-0.70	-0.69	0.50	0.62	0.64	0.42	0.43	0.43	0.45	0.48	0.50	0.47	0.44	0.36	0.38	0.56	0.53	0.46	0.45	-0.41	-0.46	-0.55	0.52	0.95	0.90	0.82	1.00						
MEDAL_1	-0.61	-0.66	-0.66	-0.65	-0.65	-0.65	-0.65	-0.65	-0.63	-0.63	0.53	0.66	0.64	0.37	0.38	0.46	0.48	0.50	0.52	0.38	0.34	0.27	0.24	0.46	0.44	0.37	0.31	-0.42	-0.47	-0.56	0.51	0.95	0.92	0.85	0.96	1.00					
MEDAL_2	-0.47	-0.54	-0.55	-0.55	-0.58	-0.57	-0.63	-0.61	-0.60	-0.60	0.62	0.75	0.74	0.41	0.41	0.47	0.49	0.54	0.60	0.30	0.28	0.18	0.10	0.40	0.40	0.30	0.20	-0.55	-0.62	-0.64	0.44	0.85	0.85	0.84	0.80	0.88	1.00				
MODAL_0	-0.56	-0.58	-0.57	-0.57	-0.56	-0.58	-0.56	-0.56	-0.52	-0.51	0.37	0.51	0.48	0.27	0.29	0.31	0.34	0.42	0.39	0.40	0.34	0.28	0.25	0.45	0.40	0.34	0.27	-0.38	-0.40	-0.48	0.50	0.76	0.71	0.65	0.85	0.86	0.75	1.00			
MODAL_2	-0.31	-0.39	-0.42	-0.44	-0.48	-0.34	-0.36	-0.32	-0.35	-0.36	0.28	0.37	0.51	0.01	0.04	0.32	0.40	0.45	0.19	0.17	0.16	0.13	0.13	0.21	0.18	0.14	0.15	-0.34	-0.41	-0.42	0.51	0.37	0.33	0.33	0.45	0.51	0.50	0.54	1.00		
RANALT_0	-0.60	-0.65	-0.65	-0.60	-0.62	-0.63	-0.65	-0.63	-0.63	-0.62	0.55	0.61	0.58	0.54	0.55	0.39	0.33	0.31	0.58	0.41	0.48	0.44	0.50	0.48	0.55	0.53	0.57	-0.36	-0.42	-0.44	0.39	0.91	0.90	0.82	0.77	0.77	0.70	0.44	0.17	1.00	
RANAL_1	-0.63	-0.70	-0.69	-0.69	-0.69	-0.67	-0.67	-0.65	-0.64	-0.64	0.59	0.67	0.66	0.61	0.62	0.38	0.33	0.31	0.65	0.45	0.52	0.51	0.53	0.54	0.62	0.62	0.62	-0.34	-0.43	-0.48	0.38	0.91	0.95	0.89	0.80	0.81	0.73	0.48	0.20	0.96	1.00
RANAL_2	-0.58	-0.66	-0.66	-0.63	-0.62	-0.67	-0.70	-0.70	-0.65	-0.64	0.67	0.76	0.75	0.75	0.76	0.33	0.27	0.26	0.78	0.47	0.53	0.49	0.48	0.59	0.67	0.65	0.63	-0.46	-0.56	-0.63	0.27	0.88	0.92	0.99	0.79	0.81	0.79	0.58	0.32	0.84	0.90
MAXSL_2	-0.15	-0.25	-0.27	-0.28	-0.23	-0.32	-0.38	-0.32	-0.29	-0.27	0.37	0.46	0.38	0.39	0.40	0.13	0.11	0.12	0.50	0.13	0.16	0.12	0.09	0.24	0.29	0.24	0.22	-0.20	-0.33	-0.28	0.08	0.60	0.61	0.63	0.51	0.55	0.64	0.35	0.31	0.62	0.62
MEDSL_0	-0.40	-0.48	-0.51	-0.46	-0.46	-0.48	-0.53	-0.52	-0.53	-0.54	0.49	0.58	0.54	0.44	0.44	0.37	0.36	0.35	0.51	0.32	0.35	0.26	0.28	0.41	0.44	0.36	0.36	-0.36	-0.42	-0.40	0.29	0.85	0.86	0.77	0.74	0.77	0.72	0.40	0.27	0.91	0.90
MEDSL_1	-0.38	-0.47	-0.45	-0.46	-0.46	-0.47	-0.51	-0.49	-0.52	-0.51	0.50	0.61	0.59	0.45	0.47	0.28	0.29	0.30	0.57	0.24	0.28	0.26	0.26	0.34	0.38	0.36	0.36	-0.31	-0.40	-0.34	0.27	0.79	0.81	0.75	0.65	0.72	0.73	0.38	0.41	0.85	0.84
MEDSL_2	-0.48	-0.55	-0.56	-0.57	-0.55	-0.55	-0.61	-0.62	-0.62	-0.63	0.57	0.68	0.65	0.49	0.51	0.37	0.36	0.37	0.62	0.25	0.32	0.28	0.26	0.37	0.43	0.41	0.38	-0.48	-0.54	-0.57	0.34	0.91	0.89	0.86	0.82	0.86	0.80	0.59	0.37	0.89	0.86
MODSL_1	-0.65	-0.70	-0.71	-0.72	-0.69	-0.69	-0.73	-0.73	-0.75	-0.75	0.60	0.68	0.65	0.46	0.48	0.41	0.43	0.44	0.58	0.36	0.41	0.36	0.40	0.46	0.50	0.47	0.48	-0.42	-0.46	-0.47	0.47	0.89	0.86	0.77	0.83	0.80	0.71	0.53	0.37	0.89	0.87
MODSL_2	-0.49	-0.56	-0.56	-0.57	-0.55	-0.60	-0.64	-0.61	-0.59	-0.59	0.58	0.68	0.66	0.50	0.53	0.30	0.31	0.34	0.65	0.27	0.33	0.31	0.30	0.38	0.45	0.43	0.42	-0.36	-0.44	-0.44	0.34	0.84	0.84	0.78	0.74	0.78	0.77	0.52	0.42	0.85	0.83
RANSL_2	-0.09	-0.19	-0.23	-0.24	-0.20	-0.26	-0.31	-0.24	-0.23	-0.21	0.31	0.41	0.33	0.33	0.34	0.11	0.09	0.11	0.44	0.11	0.14	0.10	0.08	0.20	0.25	0.20	0.19	-0.14	-0.29	-0.22	0.07	0.53	0.55	0.56	0.44	0.49	0.59	0.29	0.31	0.56	0.57
RIV_1	-0.25	-0.22	-0.14	-0.14	-0.22	-0.23	-0.17	-0.21	-0.19	-0.18	0.28	0.19	0.29	0.35	0.39	-0.06	-0.13	-0.14	0.32	0.05	0.13	0.24	0.36	0.08	0.18	0.31	0.43	-0.21	-0.28	-0.28	0.04	-0.01	-0.02	0.19	-0.07	-0.10	-0.07	-0.09	-0.03	0.06	0.04

Appendix 1.4. Correlation matrix of habitat variables with significantly different medians between pairs which laid early or late in the season (see Table 9.7)

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